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NITROGEN DYNAMICS IN UPLAND AND PEATLAND BOREAL SHIELD SOILS BEFORE AND AFTER CLEARCUTTING

BY

CHERIE JENNIFER WESTBROOK

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements of the degree of MASTER OF SCIENCE

in

ENVIRONMENTAL BIOLOGY AND ECOLOGY

DEPARTMENT OF BIOLOGICAL SCIENCES

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ABSTRACT

Patterns of nitrogen (N) dynamics among upland deciduous and conifer stands and peatlands were measured before and after clearcutting in three Boreal Shield catchments. Net mineralization and nitrification rates did not differ among forest stands due to similar soil C and N content, pH, moisture and temperature. Gross mineralization and nitrification rates were generally 10 to 100 times larger than net rates. Gross nitrification rates were higher in the recently logged conifer stand and peatland compared to the uncut stands. However, net nitrification remained low because nitrate limited conditions led to 100% immobilization. Examination of net mineralization and nitrification rates in conifer regeneration plots of varying ages showed elevated net nitrification but not mineralization rates in 2 and 11 yr old conifer stands. No coincident increase in soil nitrate was observed. These data imply a low potential for N loss post-harvest and little change in N availability for regenerating vegetation.

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **NITROGEN DYNAMICS IN UPLAND AND PEATLAND BOREAL SHIELD SOIILS BEFORE AND AFTER CLEARCUTTING** submitted by **CHERIE JENNIFER WESTBROOK** in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE** in **ENVIRONMENTAL BIOLOGY AND ECOLOGY**.

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Date Jul 27/00

In loving memory of

JACK GIBBINS

and

EDETH WESTBROOK

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CHAPTER 1: INTRODUCTION

1.0 Project Rationale

Despite considerable research on soil nitrogen (N) dynamics, our ability to predict forest N export both before and after clearcut logging is very poor. Much of the available information comes from studies of soil N dynamics in individual plots or stands in a variety of forest types (Davidson et al. 1992; Reich et al. 1997; Stark and Hart 1997). These studies are usually focussed on the upland components of the landscape and have rarely investigated wetland components (e.g. Hill and Shackleton 1989; Zak and Grigal 1991; Devito et al. 1999; Wilson et al. 1999). Furthermore, studies that evaluate clearcutting effects on soil N transformations tend to compare uncut and cut plots or stands (Vitousek and Andariese 1986; Frazer et al. 1990; Piatek and Allan 1999; Carmosini 2000) rather than measuring N transformation rates before and after logging at the same site. Alternatively, laboratory studies are used to determine potential N transformation rates under regulated environmental conditions (e.g. Vitousek et al. 1982). As a result, few studies have linked soil N processes in individual forest types at a landscape scale (Trettin et al. 1997).

To be able to "scale-up" from individual forested plots or forest stands to the landscape, we must better understand contrasts in N dynamics among all the various forest types (or landscape units) that comprise a particular ecosystem, and interactions among forest types within and between catchments. Contrasts in N cycling rates and soil N availability among upland landscape units have been linked to differences in soil organic matter content, litter N content, tree species distribution, soil C/N ratios, antecedent conditions, temperature and topographic position (Hill and Shackleton 1989; Zak and Grigal 1991; Stottlemyer et al. 1995; Chapin 1996; Lamontagne 1998; Devito et al. 1999; Min et al. 1999; Ohrui et al. 1999). In comparison, wetland N dynamics are a function of hydrological condition, which regulates the moisture regime and the degree of soil anoxia (Devito and Dillon 1993; Hill and Devito 1997). If we have a better understanding of how the abiotic and biotic processes control the consumption and release of N within forest soils, we should be able to better predict the influence of clearcutting on the landscape.

Studies of the impacts of timber harvesting on soil N dynamics have largely focussed on tropical, temperate and northern-temperate deciduous forests (Likens et al. 1978; Hendrickson et al. 1989; Adams and Attiwill 1991; Munson and Timmer 1995). Few studies have been conducted in the boreal forest, despite its global importance and change in harvesting pressure. Within the boreal forest, the Boreal Shield region of Canada is characterized by a complex landscape of peatlands and coniferous and deciduous uplands. Boreal regions are thought to rapidly cycle a relatively small pool of N (Stottlemyer et al. 1995), thus even a small loss of N after logging, through biomass removal or leaching losses, can represent a significant portion of the N pool. This may affect future forest productivity and alter N inputs to adjacent streams and lakes. Consequently, characterization of the impacts of clearcutting on soil N transformations is needed in the nutrient-poor Boreal Shield region.

1.1 Contribution to the Coldwater Lakes Project

This thesis was conducted at the Coldwater Lakes Experimental Watersheds in northwestern Ontario, Canada. The Coldwater Lakes project was initiated in 1990 to experimentally evaluate the effects of logging on Boreal Shield lake ecosystems, and to provide information about the effectiveness of shoreline buffer strips to prevent those effects. The amount that logging alters soil nutrient mobility, catchment hydrology and hydrochemistry will determine the extent that logging affects lake ecosystems. The inputs of nutrients and sediments from terrestrial systems to lakes vary seasonally and spatially due to differences in vegetation, peatland connectivity to lakes, and climate. My project contributes to the overall Coldwater Lakes research goal by assessing the spatial patterns of upland and peatland soil N dynamics before and after logging, including the mobility of N in the important forest types in this region.

1.2 Objectives

The overall objective of this thesis is to identify patterns of N dynamics in headwater catchments of the Boreal Shield before and after clearcut logging. Chapters 2

and 3 will address the overall objective, however, each chapter will focus on different problems. Chapter 2 examines patterns of net mineralization rates before and after clearcutting in conifer and deciduous upland stands and peatlands using three approaches. One, N dynamics were investigated two summers before and one summer following a late spring cut in conifer, deciduous and peatland forest types of one reference and two experimental catchments in the study area. Two, selected uncut and cut conifer stands and peatlands were used to investigate the effects of clearcutting-induced changes in soil temperature on net mineralization and nitrification rates. Reciprocal transplants were used to achieve this goal. Three, regenerating conifer stands of varying ages were used to investigate long-term patterns of N availability and transformation rates. Chapter 3 investigates gross mineralization and N immobilization rates relative to net rates in uncut and logged conifer stands and peatlands. Both chapters are presented as individual research papers. Chapter 4 will synthesize the findings of chapters 2 and 3. Implications of the findings for forest N export and site N fertility are discussed.

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CHAPTER 2: NET NITROGEN TRANSFORMATIONS BEFORE AND AFTER CLEARCUTTING IN UPLAND AND PEATLAND BOREAL SHIELD SOILS

2.0 Introduction

Studies looking at the impacts of timber harvesting on soil nitrogen (N) dynamics have largely focussed on tropical, temperate and northern-temperate deciduous forests (Likens et al. 1978; Hendrickson et al. 1989; Adams and Attiwill 1991; Munson and Timmer 1995). Few studies have been conducted in N-poor, acidic boreal forests despite the fact that boreal forests are one of the largest forested ecosystems in the world and are under intense harvesting pressure. For example, 1.2 million ha of forest was harvested in Canada in 1997; 17% of it in the Boreal Shield region, in the province of Ontario (Government of Canada 1999). The Boreal Shield forest may respond differently to clearcutting than other forested ecosystems due to cold temperatures, a relatively short growing season, low soil N content, and low atmospheric N deposition.

Before the response of soil N dynamics to clearcutting in small catchment ecosystems can be assessed, the natural spatial and temporal variation in N dynamics must be accurately determined. The Boreal Shield region is characterized by a complex landscape of peatlands and coniferous and deciduous uplands. Patterns of soil N availability and inorganic N form in upland stands have recently been associated with tree species distribution in temperate and boreal forests (Min et al. 1999). Contrasts in N transformation rates and availability between conifer and deciduous soils have been linked to differences in soil organic matter content, litter N content, C/N ratios, moisture, temperature and topographic position (Hill and Shackleton 1989; Zak and Grigal 1991; Stottlemyer et al. 1995; Chapin 1996; Lamontagne 1998; Devito et al. 1999; Ohrui et al. 1999). In comparison, N dynamics in peatlands may be more a function of the hydrological condition, which regulates the moisture regime and the degree of soil anoxia (Devito and Dillon 1993; Hill and Devito 1997). Interannual patterns of soil N cycling rates in all forest types are regulated by differences in soil moisture and temperature, driven by climate variations (e.g. Devito et al. 1999). Thus, landscape diversity in forest

communities and soil properties are expected to contribute to the spatial pattern of N dynamics within the Boreal Shield region.

Boreal forests are thought to rapidly cycle a relatively small pool of N (Stottlemyer et al. 1995), thus even a small loss of N, through biomass removal or leaching losses, can represent a significant portion of the soil N pool. Temperate and northern-temperate conifer and deciduous upland forest soils generally show elevated net mineralization and nitrification rates immediately following and up to three years after cutting, resulting in appreciable harvest-related losses of N in surface waters draining to adjacent streams and lakes (Likens et al. 1978; Vitousek et al. 1979; Feller and Kimmins 1984; Hendrickson et al. 1989; Reynolds et al. 1999). Higher N cycling rates in temperate forests after clearcutting have been attributed to physical and chemical changes in the soil. Specifically, canopy removal causes a drastic reduction in evapotranspiration that results in higher soil moisture (Likens et al. 1978; Adams et al. 1991). Higher soil moisture after logging may relieve plant and microbial water stress in well-drained upland soils, thereby accelerating mineralization and nitrification rates. Elevated soil temperature due to increased insolation (Vitousek et al. 1979) may increase mineralization and nitrification rates. Also, increases in pH of acidic soils may lead to increased decomposition of the organic-rich forest floor and logging residues (Paavolainen and Smolander 1998; Smolander et al. 1998). Few studies in temperate forests have linked the effects of clearcutting on soil N processes in individual forest types at a landscape scale (Trettin et al. 1997). Generalizing the effects of clearcutting on soil N dynamics from temperate forests to the Boreal Shield forest requires a more thorough understanding of the role of differences in physical, chemical and microclimatic soil characteristics. Such an understanding of the impacts of tree removal on soil N dynamics is necessary for effective management to prevent N losses from catchments to streams and lakes and sustain forest productivity after logging through improved soil nutrient status.

Peatlands are critical in regulating terrestrial N loss to adjacent water bodies because of their abundance and location in the landscape, connecting them hydrologically to uplands and streams. The effects of clearcutting on soil N dynamics in undrained peatlands, particularly those in the boreal forest, have yet to be examined. Clearcutting

potentially has both direct and indirect impacts on N cycling in peatlands. Direct impacts of logging include increased soil temperature and physical disturbance such as rutting and compaction (Grigal and Brooks 1997; Groot 1987). Higher temperatures observed at the surface of clearcut peatlands in northern Michigan have been correlated with increased cellulose decomposition (Trettin et al. 1997), which may lead to a build-up of NH_4^+ in the surface peat. Rutting and compaction may alter water flowpaths and thus biogeochemical cycling of soil nutrients. Indirect impacts include increased N inputs from adjacent uplands and a higher water table due to reduced evapotranspiration and increased runoff from the contributing catchment area (Roy et al. 1997; Groot 1998).

Seasonal and annual wetting and drying cycles confound problems in predicting post-harvest water table elevations and associated soil N dynamics. Aerts et al. (1992) suggests that increased N inputs, through high atmospheric deposition, to oligotrophic bogs may increase their productivity and the rate of decomposition. In fact, Rochefort et al. (1990) have shown increased growth of *Sphagnum* with addition of low levels of N. As logging has been shown to increase N mobility in the uplands of other forests, increased nutrient input to boreal peatlands may result in comparable increases in productivity and decomposition, even if the peatland is not logged. Water table position can influence soil N transformations within peatlands by regulating the soil redox status (Walbridge and Lockaby 1994). It is unclear how the direct and indirect factors potentially altered by clearcutting interrelate to govern N availability and transformation rates in northern peatlands.

To evaluate short-term effects of logging and asses how this may vary among upland deciduous and conifer stands and peatlands within small headwater catchments, net N mineralization rates, nitrification rates, and soil N were examined in three Boreal Shield catchments. Net mineralization and nitrification rates and soil inorganic N were measured for two summers before and for the summer immediately following a late spring clearcut. As clearcutting can increase the production and leaching of organic N from forest soils, particularly peatlands (Nieminen 1998), soil DON was measured for selected conifer and peatland sites within the study catchments for two months in reference (uncut) and logged peatlands. It was expected that mineralization and

nitrification rates would be highest in deciduous stands, intermediate in conifer stands and lowest in the peatlands. Nitrate availability was expected to follow a similar trend, while NH_4^+ availability was expected to be highest in the peatlands. Clearcutting was hypothesized to increase mineralization rates, nitrification rates and inorganic and organic N in all forest types. If these differences were observed, they were expected to be influenced by clearcutting-induced changes in soil temperature, moisture, pH and C/N ratios. As temperature was the primary factor differing between uncut and logged conifer stands and peatlands, a field transplant experiment of uncut and clearcut soils was used to test the effect of temperature on mineralization and nitrification rates. Soils incubated at higher temperatures were hypothesized to have higher mineralization and nitrification rates. To determine how long the effects of clearcutting may persist in boreal conifer stands, I examined mineralization and nitrification rates and N availability using a regeneration chronosequence, of 4 stands ranging in age from 0 to 64 yrs after logging. I hypothesized that there would be a time lag before increases in net mineralization and nitrification rates are observed, and that soil N would increase within the first year after tree removal due to reduced plant uptake (Nieminen 1998).

2.1 General Site Description

This research was conducted between May 1996 and October 1998 at the Coldwater Lakes Experimental Watersheds (49°05'N and 92°10'W), situated on the Precambrian Shield in northwestern Ontario (Figure 2-1 inset). The study site is located in the Boreal Shield region (Figure 2-1 inset). Mean annual precipitation in Atikokan, about 70 km south of the study site, is 550 mm with 31.5 % falling as snow (C. Allan, pers. comm.). April to October rainfall was 587 mm in 1996, 409 mm in 1997 and 506 mm in 1998 (R. Steedman, unpubl. data). Water equivalency of the late winter snowpack was about 130 mm in both 1996 and 1997, and only 5 mm in 1998 (C. Allan, unpubl. data). The mean January and July air temperatures are –17.6°C and 19.2°C, respectively (R. Steedman, unpubl. data). Average N deposition (1970-1982) at the nearest recording

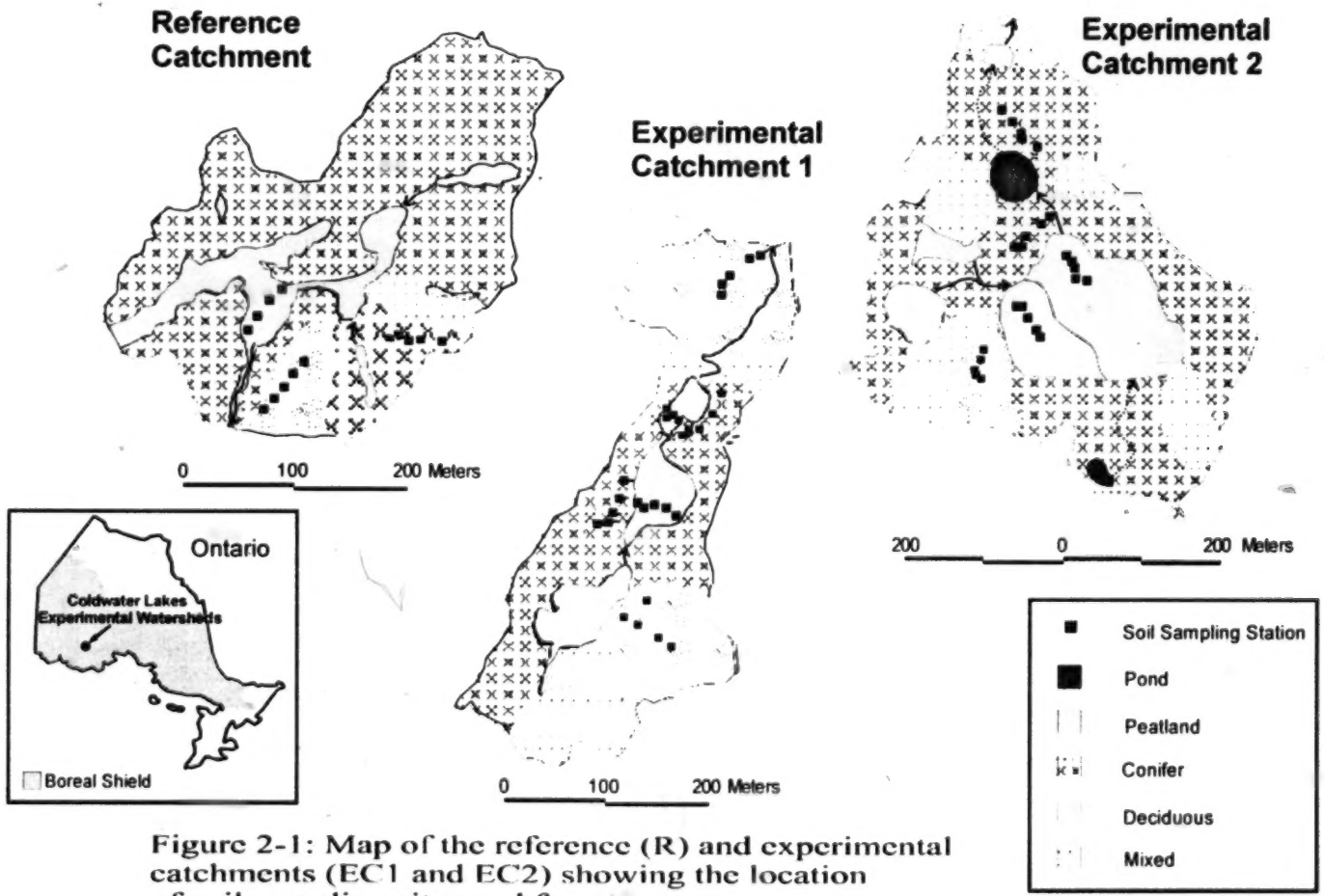

Figure 2-1: Map of the reference (R) and experimental catchments (EC1 and EC2) showing the location of soil sampling sites and forest cover.

station located at the Experimental Lakes Area (ELA), about 350 km northwest of the study site, is 2.0 ± 0.8 kg/ha of NH_4^+-N and 1.8 ± 0.5 kg/ha of NO_3^--N (Linsey et al. 1987).

The bedrock geology of the study area is Archean granitic-gneissic and the Hartmann moraine runs along the southwest section of the study region (Zoltai, 1965). Upland soils in the study area are classified as orthic dysteric brunisols. Bouldery glacial till is patchy and thin near the top of hillslopes and occasionally exceeds 1 m at the base of hillslopes. The acidic forest floor (LFH horizon) is generally between 3 and 8 cm thick in unlogged stands and is 0 to 8 cm thick in logged stands. Mineral layers are comprised of silty loam to coarse sand and are probably of glacial-fluvial origin. The top 20 cm of peatland soils consist of a fibrous root mass, underlain by partially-decomposed, fibric organic material, and covered by thick moss (*Sphagnum* spp.) mats.

Undisturbed upland areas are composed of relatively even-aged deciduous and conifer stands and are approximately 80-120 yrs old as natural fires are frequent in the region. A stand was defined in this study to be >60% of either conifer or deciduous trees > 50 cm tall. Conifer stands and peatlands are the dominant forest types in this landscape. Peatlands comprise approximately 15-35% of the catchment area, occurring along a series of terraces along main flow channels. The major tree species in the conifer stands are jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP). The peatlands are dominated by black spruce with some black ash (*Fraxinus nigra* Marsh.) and an understory of the shrubs *Chamaedaphne calyculata* and *Ledum groenlandicum*. Deciduous stands are comprised mainly of trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera*) with a speckled alder (*Alnus incana* ssp. *rugosa*) understory.

2.2 Experimental Design

Three different experiments were used to assess potential clearcutting impacts on soil N dynamics in this system. One, N transformation rates were investigated before and

immediately following logging in conifer, deciduous and peatland forest types of one reference and two experimental catchments of the Coldwater Lakes Experimental Watersheds. This study is referred to as the catchment study throughout this paper. Two, selected uncut and logged conifer stands and peatlands were used to estimate the effects of temperature on net mineralization and nitrification rates. To do this, a reciprocal transplant design was used. This reciprocal transplant study tests for temperature controls on N cycling rates. Three, to determine how long logging-induced changes in soil net N transformation rates may persist in boreal conifer stands, I examined net mineralization and nitrification rates in a clearcut chronosequence, with stand ages ranging from 0 to 64 yrs after logging. This study is hereafter referred to as the regeneration study.

2.2.1 Catchment Study

The spatial distribution of N mineralization and nitrification before and after logging was measured in 3 sub-catchments of Lakes 20, 26 and 39 in the study area. A sub-catchment of Lake 20 was a reference catchment (R) and the whole Lake 20 catchment remained unlogged for the duration of the study. The uplands adjacent to Lakes 26 and 39 were commercially logged by Buchanan Forest Products Ltd. in the summer of 1996, with the exception of the 2 sub-catchments. Tree removal was done with a feller-buncher and chainsaws, and logs were dragged to loading docks with cable skidders. Experimental catchment 1 (EC1), a sub-catchment of Lake 26, and experimental catchment 2 (EC2), a sub-catchment of Lake 39, were logged by chainsaw using cable skidders during June and July 1998. All peatlands were logged in EC1, but two peatlands were not logged in EC2 because the trees were too small to be merchantable. Slash was removed from the logged conifer stands and peatlands while the crowns of deciduous trees remained in the logged deciduous stands. Figure 2-1 illustrates transect location and forest cover of each catchment and general soil characteristics are presented in Table 2-1.

Within each study catchment, 1 or 2 transects were selected in each forest type, depending on the extent of forest type coverage per catchment (Figure 2-1). The standard

Table 2-1: Mean (+ SE) soil carbon to nitrogen ratios, pH and bulk density for each forest type within each catchment for 1997 (before clearcutting) and 1998 (after clearcutting the experimental catchments). n=2-4 for C/N ratios and n=4-10 for pH and bulk density values.

Forest Cover	Catchment	C/N ratio 1997	C/N ratio 1998	pH 1997	pH 1998	Bulk Density (Mg/m^3) 1997	Bulk Density (Mg/m^3) 1998
Forest Floor							
Conifer	R	31.3 ± 0.2	31.3 ± 0.1	4.02 ± 0.18	3.94 ± 0.09	0.13 ± 0.02	0.17 ± 0.03
	EC1	37.5 ± 1.6	37.9 ± 0.5	3.83 ± 0.07	3.94 ± 0.08	0.20 ± 0.03	0.17 ± 0.02
	EC2	37.5 ± 0.5	40.1 ± 1.6	3.84 ± 0.09	3.99 ± 0.06	0.15 ± 0.01	0.22 ± 0.04
Deciduous	R	28.3 ± 0.2	28.0 ± 0.0	4.02 ± 0.07	4.04 ± 0.04	0.16 ± 0.03	0.19 ± 0.02
	EC1	26.7 ± 0.4	36.0 ± 3.5	4.42 ± 0.17	4.51 ± 0.08	0.18 ± 0.02	0.28 ± 0.06
	EC2	29.8 ± 0.4	30.6 ± 0.1	4.27 ± 0.05	4.29 ± 0.06	0.18 ± 0.02	0.27 ± 0.02
Peatland	R	27.7 ± 1.9	25.9 ± 0.0	4.10 ± 0.06	4.21 ± 0.02	0.04 ± 0.01	0.04 ± 0.01
	EC1	33.5 ± 1.2	42.2 ± 2.9	4.16 ± 0.08	4.13 ± 0.04	0.07 ± 0.01	0.14 ± 0.03
	EC2	52.5 ± 0.7	48.7 ± 0.0	3.89 ± 0.09	3.83 ± 0.05	0.06 ± 0.01	0.07 ± 0.02
0-10 cm Mineral							
Conifer	R	25.1 ± 0.2	22.6 ± 0.2	4.22 ± 0.16	4.37 ± 0.11	0.53 ± 0.06	0.46 ± 0.06
	EC1	30.9 ± 1.7	26.2 ± 0.7	4.05 ± 0.08	4.04 ± 0.09	0.47 ± 0.02	0.58 ± 0.08
	EC2	30.3 ± 0.9	26.9 ± 0.2	3.97 ± 0.12	3.97 ± 0.13	0.51 ± 0.02	0.53 ± 0.06
Deciduous	R	25.0 ± 0.2	25.5 ± 0.5	4.05 ± 0.05	4.10 ± 0.08	0.35 ± 0.05	0.50 ± 0.10
	EC1	25.6 ± 2.4	21.5 ± 0.1	4.48 ± 0.10	4.35 ± 0.08	0.48 ± 0.03	0.55 ± 0.06
	EC2	26.3 ± 0.0	20.9 ± 0.4	4.41 ± 0.14	4.16 ± 0.12	0.54 ± 0.04	0.54 ± 0.05

buried bag technique (Eno 1960), described later, was used to measure soil N, net mineralization and nitrification rates at 5 sites, spaced 20 m apart, along each transect monthly during the snow free season (Figure 2-2). For this chapter, values for the first of July to the end of October for 1996 though 1998 are compared as soil was sampled from July to October in 1996, and the forest cover in EC1 and EC2 was not logged until late June – early July 1998. Availability and mobility rates of dissolved organic N (DON) production (from TDN minus TIN measurements) were estimated on two occasions, immediately following logging in July 1998 and again in September 1998. These measurements were made at 5 sites in the conifer stands and peatlands of the R and EC2 to provide an indication of the importance of organic N to soil N dynamics in this ecosystem.

2.2.2 Reciprocal Transplant Study

To determine the influence of soil temperature in uncut and logged upland conifer stands on net mineralization and nitrification, a one-month long reciprocal transplant experiment was conducted in each of June and September 1997. The mineralization rates of 0-10 cm mineral soil in an uncut stand of EC1 were compared to 0-10 cm mineral soil in an adjacent cut block that had the organic forest floor removed by heavy mechanical disturbance. There was no regenerating vegetation at the heavily disturbed site by August 1997. Five polyethylene bags from the highly disturbed location were reciprocally transplanted in uncut sites, where the forest floor was placed on top for the duration of the incubation (Figure 2-3). At EC2, uncut forest floor soil was reciprocally transplanted to an adjacent, minimally impacted logged stand, where the forest floor was present. Naturally regenerating vegetation, predominately aspen <50 cm in height, covered 40% of the minimally disturbed logged stand by August 1997.

A second transplant experiment was conducted in uncut and logged conifer (forest floor and 0-10 cm mineral) stands and peatlands (top 10 cm of peat) in August 1998 (i.e. 2 months after clearcutting). Less than 10% of the logged conifer transect was covered with new growth, predominately various ferns and aspen suckers, by the end of August

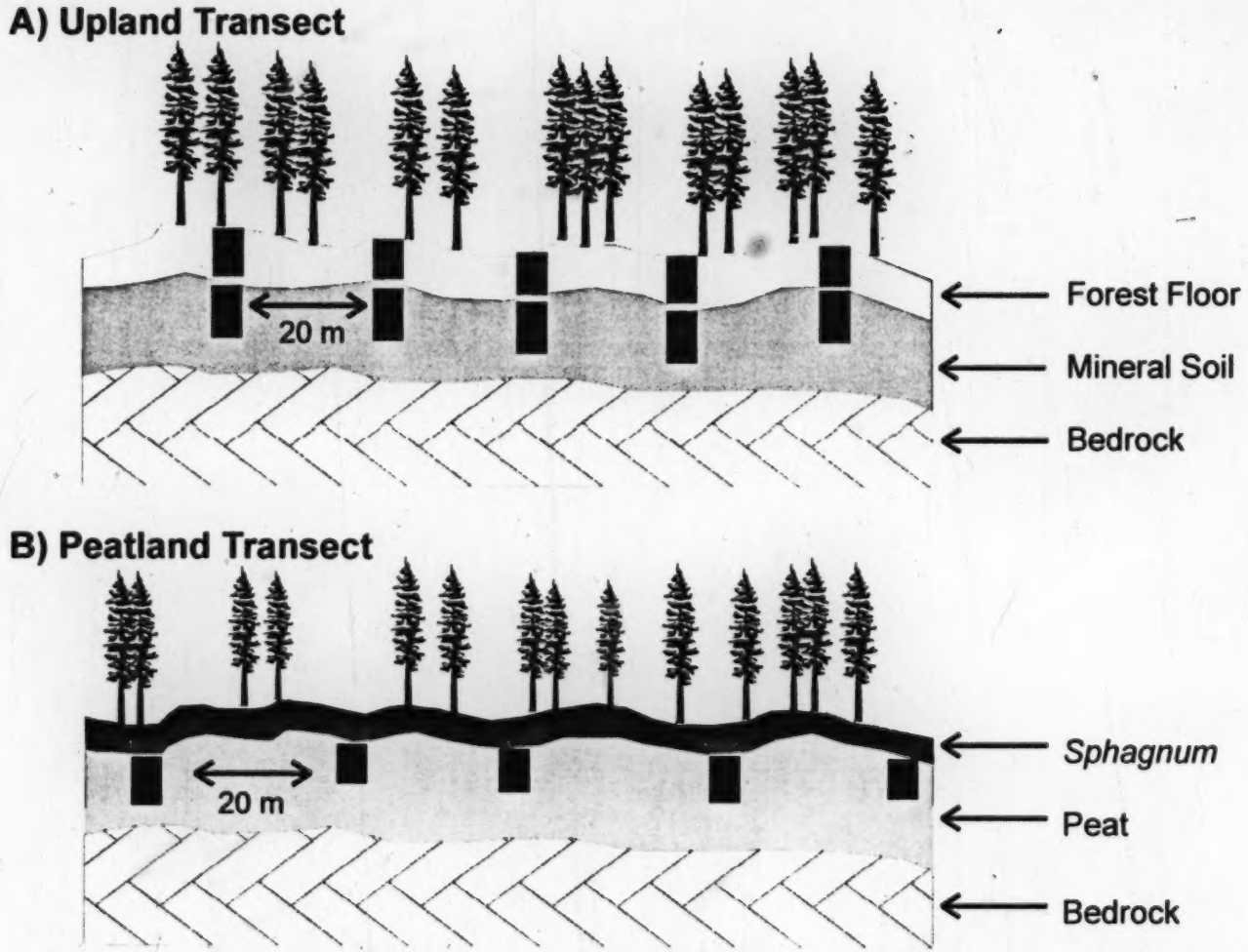

Figure 2-2: Schematic cross-section a transect in an A) upland (conifer or deciduous) stand and B) peatland. Black rectangles represent location of soil cores. Soil cores are generally 10 cm long in mineral soil and peatlands, and the entire length of the forest floor (1-10 cm thick).

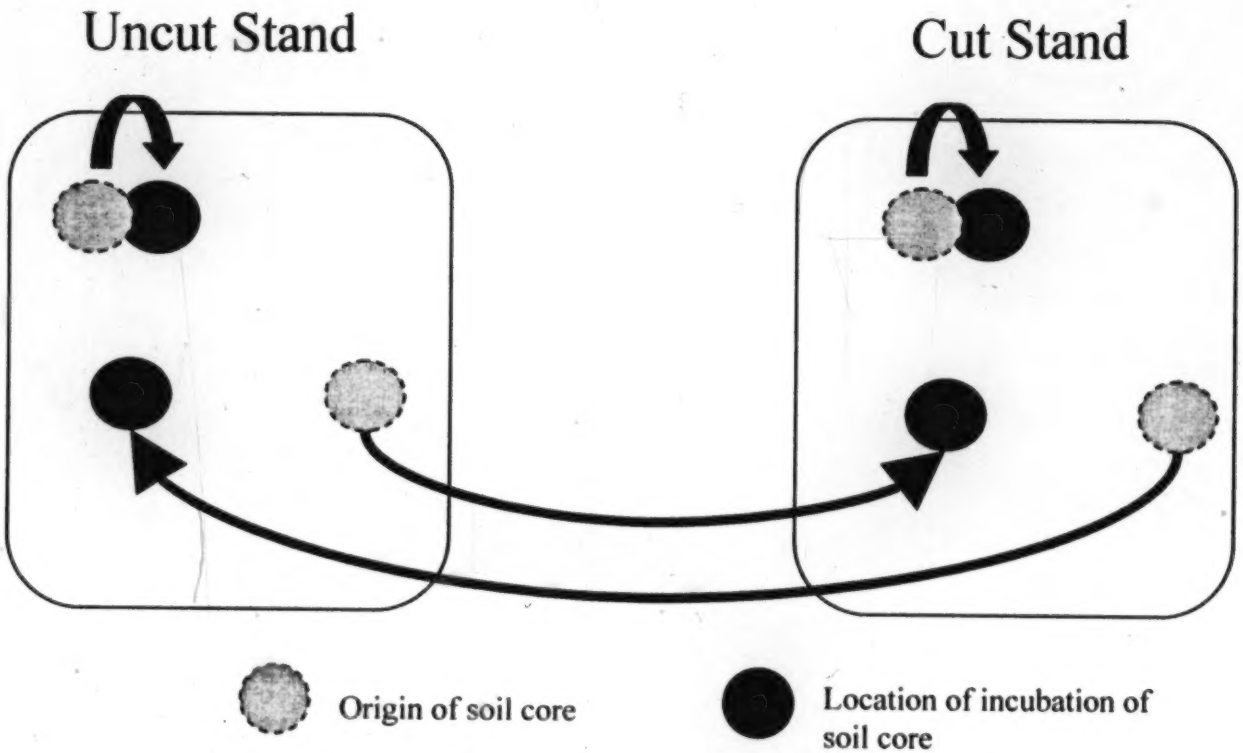

Figure 2-3: Schematic of the experimental design for the reciprocal transplant study. Arrows indicate where soils are removed from and where they are incubated.

1998. Regenerating *Sphagnum* sp. (on peatland hummocks) and various graminoids and sedges covered about 20% the logged peatland soil. Ten soil samples were transplanted from each uncut and logged stand. Temperature was measured once at the beginning and end of each incubation period with a hand-held thermistor during the 1997 and 1998 transplant experiments. Hourly measurements of soil temperature were conducted at one location along each logged and uncut transect with HOBO data loggers.

2.2.3 Regeneration Study

Study sites consisting of paired 0, 2, 11, 15 and 64 yr regenerating stands and 100-120 yr old uncut stands, located within 25 km of each other, were chosen along the Hartmann moraine. The 11 yr and 64 yr regenerating stands shared an uncut stand due to their close proximity. The uncut stands were approximately 100-120 yrs old, succeeding from fire disturbance and were predominately jack pine with some black spruce. The 0 yr regenerating stand was the logged conifer stands in the catchment study, described earlier. Both the 11 yr and 15 yr regenerating stands were replanted to jack pine two years after logging while the 64 yr regenerating stand naturally regenerated a mix of jack pine and black spruce. Sparse conifer seedlings were observed at the 2 yr regenerating stand and the soil was mostly barren. Patches of the forest floor were missing at three of the sites in the 2 yr regenerating stand. The forest floor was completely removed by scarification before planting in the 15 yr logged stand, and the trees were thinned 5 yrs after planting.

Transects of 7 soil sampling sites approximately 20 m apart were located in each uncut and regenerating stand. At each site, forest floor (where present) and 0-10 cm mineral soils were sampled for NH_4^+-N, NO_3^--N, temperature, volumetric soil moisture and other soil properties from 01 July to 26 September 1998. A total of three, about 30 d, incubations were done to measure mineralization and nitrification rates.

2.3 Methods

2.3.1 Soil Chemistry and Physical Properties

Soil sampling and incubation experiments were conducted in a similar manner in the catchment, reciprocal transplant and regeneration studies. At each sample site, soil cores sampled with a 4 cm diameter stainless steel bulb corer were collected at 2 depth increments in the upland soils (forest floor and 0-10 cm mineral soils) and at 0-10 cm in the peatland hollows. During the catchment study in 1996, soils were sampled with the same bulb corer at two – 10 cm depth increments. The forest floor is generally <10 cm thick in the conifer and deciduous stands. Consequently, the surface 10 cm increment included both the forest floor and a small portion of the underlying mineral soils during the 1996 sampling year. Consequently, 1996 data are presented here as preliminary data to provide an indication of the interannual variation in N mineralization and nitrification rates. Soil cores were placed in 0.025 mm polyethylene bags and incubated cores were returned to the soil for 4 weeks. As mineralization rates were linear within the buried bags over 4-6 weeks, a 4 week incubation was deemed an appropriate length of time to measure mineralization rates using this technique (Appendix A). Initial cores were kept on ice in the field and returned to the field lab where they were kept at 4 °C until processing, within 24 h of sampling. Samples taken in 1996 were shipped on ice to the University of Toronto Biogeochemistry lab for processing and were analyzed within 72 h of sampling. Quality control analyses found no difference in extractable N between samples extracted within 24 h and those extracted 72 h after sampling (Appendix B).

For each initial and incubated soil core, inorganic N in an approximately 5 g (dry wt.) sub-sample was extracted with 50 mL 2 M KCl and shaken reciprocally for one hour. Extracts were gravity filtered through pre-washed (with distilled water) Fisherbrand 1 µm filter paper and frozen until analyzed for NH_4^+-N and NO_3^--N content on an autoanalyzer (Technicon, 1973a, b). Estimates of net nitrification were determined by the difference in NO_3^--N content between the incubated and initial cores (Eno 1960). Net mineralization was estimated by the inorganic-N content (NH_4^+-N + NO_3^--N) of the incubated core minus that in the initial core. The extracts were subsampled in 1998 for total dissolved N

(TDN) during the July 5 to August 2 and August 30 to September 25 incubations. TDN in the soil extracts was photocombusted to NO_3^- using a short UV irradiator, followed by a Zn reduction to NH_4^+. Ammonium-N content of the extracts was then analyzed on a Technicon Autoanalyzer at the Limnology Laboratory, University of Alberta, Edmonton, Alberta. TDN mobilization was determined by the difference in TDN content between the initial and incubated cores.

Soil temperature was measured with a hand-held thermistor at each sampling site and soil depth at the start of each incubation period. Moisture was determined by oven drying (105°C for 24 h) a sub-sample of soil from each sampling site and depth for each date, with percent moisture equal to the gravimetric moisture multiplied by soil bulk density. Soil acidity was measured as pH in a 5:1 water:soil slurry with a glass electrode for one sample date in the regeneration study, and once before and after logging in the catchment study. Bulk density was calculated from the dry mass/total core volume over the course of each study. The mean bulk density for each site along a transect was calculated for uncut and logged soils, and was used to convert soil N concentrations from a per gram basis to a per hectare basis to facilitate comparison with other published studies. The measured bulk densities do not account for larger rock fragments and boulders common in the glacial till for this area. Total C and N were determined for two replicates of a composite sample from each transect at the catchment sites in August 1997 (before logging) and October 1998 (after logging). Total C and N were analyzed on a Carlo-Erba NA 1500 C/N Analyzer (Carlo-Erba Strumentazione, Italy) connected to an isotope ratio mass spectrometer at the Soil Biochemistry Laboratory, University of Alberta.

Forest cover type, density and diameter at breast height (DBH) was surveyed at the catchment transects within a 8 m x 8 m quadrant around each soil sampling station once before, immediately after and 2.5 months after clearcut logging. The type and approximate quantity of slash remaining after logging was recorded for each sampling site in each logged catchment.

2.3.2 Calculations

Growing season (GS) N mineralization and nitrification for the three catchments and the regeneration chronosequence figures were calculated from the sum of the means of all coring sites from each incubation period. Standard errors (SE) were calculated by first order error propagation of the standard deviation of monthly means for each forest type within each catchment in the catchment study or for each transect in the regeneration study (Meyer 1975):

$$SE = \frac{\sqrt{(\sum (S_i)^2)}}{\sqrt{n}}$$

where S_i is the standard deviation of mineralization or nitrification rates (for each forest type within each catchment) associated with each incubation period, and n is the number of months mineralization and nitrification rates were measured. For statistically purposes, growing season totals were calculated for each coring site within each forest type and catchment (catchment study) and for each site in each transect (regeneration study).

The soil N pools represent time-weighted average pool size over the 4 month (catchment study) or 3 month (regeneration study) growing season. Growing season mean temperature and volumetric soil moisture were determined by weighting for the number of days in each incubation period over the entire study period(s).

2.3.3 Statistics

All statistical tests were performed on the forest floor and the 0-10 cm mineral soils separately as it was found that most parameters differed significantly among the two soil depth increments ($P < 0.05$). For the catchment study, pre-cut patterns in mineralization and nitrification rates, soil N, temperature, moisture, pH, C/N ratio and soil bulk density among the different forest types (conifer, deciduous and peatland), among catchments (the reference and two experimental catchments) and their interaction were determined using a general linear model (GLM). When the GLM indicated a

significant forest type, specific hypotheses were tested using contrasts. Relationships among N transformation rates, N and soil physical and chemical characteristics were determined using linear regression analyses. Patterns before and after clearcutting for N transformation rates, microclimate factors and soil properties among years (before and after cutting years), catchments, forest types and their interactions using a GLM. Where the GLM indicated a significant difference between years, a posteriori contrasts were used to determine which forest types within each catchment were different in 1998 (after cutting) vs. 1997 (before cutting). Total dissolved N and total inorganic N pools and mobility differences between the reference and logged stands for peatland and conifer forest types were assessed using two-sample t-tests, adjusting the probabilities for multiple tests using the Bonferroni test. Data from the two study dates were combined as no differences were found between dates ($P > 0.10$).

In the reciprocal transplant study, differences in location of soil incubation for N mineralization, nitrification, moisture and temperature within each forest type and place of origin were assessed using two-sample t-tests, adjusting the probabilities for multiple tests using the Bonferroni test. The two study years, 1997 and 1998, were assessed separately.

For the regeneration chronosequence data, tests for linearity in rates and microclimatic factors over the various ages (i.e. along the chronosequence) within logged and uncut stands were determined with regression analyses. The effect of clearcutting status (uncut vs. logged), regeneration age and their interaction for forest floor and 0-10 cm mineral soils was assessed using ANOVA with a posteriori contrasts to test for differences between uncut and different aged regenerating stands. All tests were preformed using SYSTAT version 7 (SYSTAT Inc. 1992).

2.4 Results

2.4.1 Pre-cut Conditions

Comparisons of 1997 rates in forest floor and 0-10 cm mineral soils revealed very similar net mineralization and nitrification among replicate transects within a forest type

in each catchment (data not shown). For both mineralization and nitrification rates, using 1996 and 1997 data, no significant differences between transects were found in 9 out of 9 cases. Thus due to the similarity between transects within a forest type, transects were combined and comparisons hereafter are based on the 3 forest types within each catchment.

Forest floor mineralization rates for the 1997 growing season on a per gram soil basis show a trend of deciduous greater than conifer, although the results were not significant ($P = 0.08$) due to high variability within catchments, not between catchments. There was considerable variability within and between catchment in the peatland soil. Thus, a difference between uplands and peatlands could not be detected ($P = 0.07$) (Table 2-2). The 1997 rates were comparable to those measured in 1996, and 1996 mineralization rates tended to be higher in the deciduous stands compared to the conifer stands and highly variable in the peatlands. Within the conifer and deciduous upland stands in 1997, mineralization rates were similar among catchments ($P = 0.55$ and $P = 0.60$, respectively). Mineralization rates in the 0-10 cm mineral soils were similar for conifer and deciduous stands, and usually showed net immobilization (Table 2-2).

In general, trends among forest types and among catchments were similar when mineralization and nitrification rates were expressed on an areal basis (Table 2-3). Also, differences between forest floor and 0-10 cm mineral soils were not as great when rates were expressed on an areal basis because of the higher bulk densities of the 0-10 cm mineral soils.

The 1997 growing season total nitrification rates in forest floor and 0-10 cm mineral soils of the conifer and deciduous stands were often negative, while nitrification rates alternated between negative and positive in the peatlands (Table 2-2). There was no significant difference among the three forest types at either soil depth ($P > 0.60$) and nitrification rates were similar between soil depths. Nitrification rates in the R peatland were significantly higher than in EC1 peatlands ($P = 0.04$), but no other differences among catchments were observed. No differences in nitrification rates among catchments were observed in the forest floor soils of the conifer ($P = 0.83$) and deciduous ($P = 0.93$) stands. Similar trends were observed in the 0-10 cm mineral soils (Table 2-2).

Table 2-2: 1996-1998 growing season net N mineralization and nitrification for forest floor and 0-10 cm mineral soils within the reference (R) and experimental (EC1 and EC2) catchments. Shown are sums ± SE of monthly mean rates; GS = 01 July to 26 October.

		1996 Growing Season				1997 Growing Season				1998 Growing Season			
		N Mineralization		Nitrification		N Mineralization		Nitrification		N Mineralization		Nitrification	
Forest Cover	Catchment	µg/g		µg/g		µg/g		µg/g		µg/g		µg/g	
Forest Floor*													
Deciduous	R	35.3 ± 22.1		-0.41 ± 0.17		46.0 ± 38.2		-0.43 ± 0.38		123.4 ± 35.6		4.29 ± 0.09	
	EC1	15.1 ± 10.0		0.10 ± 0.26		91.3 ± 37.2		-0.54 ± 0.54		137.0 ± 807.3		0.13 ± 0.00	
	EC2	39.0 ± 25.6		0.26 ± 0.50		93.9 ± 57.1		-0.81 ± 0.95		-130.4 ± 1033.1		-0.23 ± 0.00	
Conifer	R	nd		nd		21.1 ± 9.9		-0.30 ± 0.23		35.3 ± 7.5		0.62 ± 0.09	
	EC1	17.9 ± 13.2		-0.05 ± 0.21		21.7 ± 13.5		-0.25 ± 1.32		91.6 ± 125.7		-0.16 ± 0.00	
	EC2	11.2 ± 6.4		-0.19 ± 0.08		30.3 ± 18.8		-0.13 ± 0.17		39.9 ± 141.1		0.04 ± 0.00	
Peatland	R	4.7 ± 104.3		-0.65 ± 0.39		129.5 ± 50.8		4.74 ± 2.64		122.9 ± 31.1		-0.33 ± 0.01	
	EC1	98.1 ± 43.5		-0.04 ± 0.30		-1.1 ± 21.0		-3.09 ± 2.63		5.2 ± 40.6		0.43 ± 0.01	
	EC2	76.5 ± 77.6		-0.82 ± 0.28		13.3 ± 14.1		1.49 ± 3.51		22.6 ± 40.3		-0.14 ± 0.00	
0-10 cm Mineral													
Deciduous	R	-16.5 ± 8.7		-0.46 ± 0.10		-3.2 ± 1.7		-0.37 ± 0.14		2.3 ± 0.5		1.50 ± 0.01	
	EC1	-5.2 ± 3.5		0.24 ± 0.35		41.8 ± 35.6		1.47 ± 1.51		-0.8 ± 0.8		0.17 ± 0.00	
	EC2	2.3 ± n/a		-0.40 ± n/a		9.2 ± 6.0		-0.24 ± 0.23		-2.2 ± 10.4		-0.15 ± 0.00	
Conifer	R	nd		nd		-6.0 ± 0.7		-0.25 ± 0.02		1.1 ± 0.3		0.46 ± 0.01	
	EC1	-10.6 ± 2.5		-0.28 ± 0.00		5.2 ± 6.1		-0.28 ± 0.32		-6.5 ± 30.2		0.05 ± 0.00	
	EC2	-10.8 ± 0.7		-0.31 ± 0.08		8.8 ± 8.2		0.14 ± 0.30		-14.0 ± 1.3		-0.04 ± 0.00	

* = for 1996, 0-10cm soil was sampled and this increment included the forest floor, which was between 3 and 8 cm thick
nd = no data
n/a = not applicable as n=1

Table 2-3: Areal estimates of 1996-1998 growing season net N mineralization and nitrification for forest floor and 0-10 cm mineral soils within the reference (R) and experimental (EC1 and EC2) catchments. Shown are sums ± SE of monthly mean rates; GS = 01 July to 26 October.

		1996 Growing Season				1997 Growing Season				1998 Growing Season			
		N Mineralization		Nitrification		N Mineralization		Nitrification		N Mineralization		Nitrification	
Forest Cover	Catchment	mg/m²		mg/m²		mg/m²		mg/m²		mg/m²		mg/m²	
Forest Floor*													
Deciduous	R	326.7 ±	321.0	-8.8 ±	2.6	608.3 ±	643.4	-4.7 ±	2.9	1965.9 ±	530.0	131.6 ±	35.6
	EC1	448.0 ±	520.7	-16.9 ±	7.0	821.9 ±	145.4	-3.7 ±	3.3	1065.6 ±	1045.6	-0.3 ±	1.0
	EC2	35.5 ±	31.5	-0.5 ±	9.0	975.4 ±	483.7	-8.1 ±	8.1	-1164.7 ±	1243.4	-3.6 ±	0.6
Conifer	R	nd		nd		162.6 ±	66.0	-2.7 ±	1.6	262.6 ±	78.8	20.7 ±	19.9
	EC1	337.4 ±	280.9	-7.0 ±	3.8	318.0 ±	187.1	-8.8 ±	7.4	962.6 ±	264.1	-1.9 ±	1.1
	EC2	859.0 ±	n/a	-17.0 ±	n/a	324.6 ±	131.6	-1.6 ±	0.4	1505.4 ±	921.1	-1.8 ±	1.0
Peatland	R	26.2 ±	51.6	-5.0 ±	2.0	442.3 ±	296.7	12.9 ±	11.7	406.5 ±	188.8	-6.1 ±	4.1
	EC1	31.4 ±	n/a	-5.7 ±	n/a	1.2 ±	107.1	-15.4 ±	5.2	189.8 ±	252.3	4.9 ±	3.3
	EC2	281.7 ±	216.5	-3.8 ±	1.1	96.2 ±	64.1	14.9 ±	14.4	204.6 ±	206.0	-0.3 ±	1.0
0-10 cm Mineral													
Deciduous	R	-998.3 ±	383.2	-24.8 ±	1.6	-101.3 ±	65.4	-8.0 ±	3.5	-83.0 ±	211.1	96.5 ±	30.7
	EC1	-234.9 ±	181.5	14.4 ±	13.9	1034.8 ±	960.9	77.0 ±	52.2	-124.3 ±	144.8	8.3 ±	4.0
	EC2	-3.8 ±	n/a	-26.7 ±	n/a	382.6 ±	204.8	-5.9 ±	7.8	-10.7 ±	338.2	-6.0 ±	0.4
Conifer	R	nd		nd		-291.1 ±	78.4	-12.9 ±	0.7	39.6 ±	38.1	28.3 ±	27.5
	EC1	95.6 ±	n/a	-15.9 ±	n/a	163.3 ±	89.0	0.2 ±	5.2	-489.0 ±	961.0	2.1 ±	4.3
	EC2	-1428.7 ±	n/a	-57.8 ±	n/a	486.9 ±	285.1	9.7 ±	10.4	-667.0 ±	237.4	-0.6 ±	2.2

* = for 1996, 0-10cm soil was sampled and this increment included the forest floor, which was between 3 and 8 cm thick.
nd = no data
n/a = not applicable as n=1

Nitrification rates calculated on an areal basis follow a similar trend to those calculated on a per gram basis (Table 2-3).

The general trends in soil NH_4^+-N between catchments and years was similar for the forest floor and 0-10 cm mineral soils, although soil NH_4^+-N calculated on a per gram basis was larger in the forest floor soils (Figure 2-4). During the 1997 pre-cutting period, little difference between conifer and deciduous stands, or among catchments was measured. However, peatland NH_4^+-N was 50 % higher than that in conifer and deciduous soils ($P < 0.001$). Also, a statistically significant, but small difference was found for soil NH_4^+-N among catchments for the peatlands ($P < 0.001$). Forest floor NH_4^+-N was similar to that in 0-10 cm mineral soils (Figure 2-4).

Soil NO_3^--N was relatively low and differed among catchments within each forest type for forest floor ($P < 0.001$) and 0-10 cm mineral soils ($P < 0.001$) (Figure 2-5). The range in soil NO_3^--N among the three catchments is similar for the deciduous and conifer soils. Peatland NO_3^--N appear to be slightly higher than that in the conifer and deciduous upland forest floor soils.

Mineralization rates (on a per gram basis) for all uncut sites in 1997 and 1998 showed a low but significant negative correlation with soil C/N ratios ($r = -0.404$, $P < 0.001$) and a positive correlation with soil C content ($r = 0.455$, $P < 0.001$), N content ($r = 0.531$, $P < 0.001$), pH ($r = 0.711$, $P < 0.001$), moisture ($r = 0.448$, $P < 0.001$) and temperature ($r = 0.535$, $P < 0.001$). Nitrification rates were negatively correlated to NO_3^- ($r = -0.344$, $P = 0.030$). Soil NH_4^+ was positively correlated with temperature ($r = 0.310$, $P = 0.038$) and moisture ($r = 0.743$, $P < 0.001$). Soil NO_3^- was positively related to moisture ($r = 0.458$, $P < 0.001$). In the peatlands, growing season mean water table elevations were positively related to mineralization rates ($P = 0.021$) but not to nitrification rates ($P = 0.589$).

2.4.2 Clearcutting in Uplands and Peatlands

Growing season mean soil temperatures were 3-7°C higher in 1998 compared to mean temperatures in 1997 (Figure 2-6), thus higher mineralization rates were expected in all soils due to the positive correlation between mineralization rates and temperature

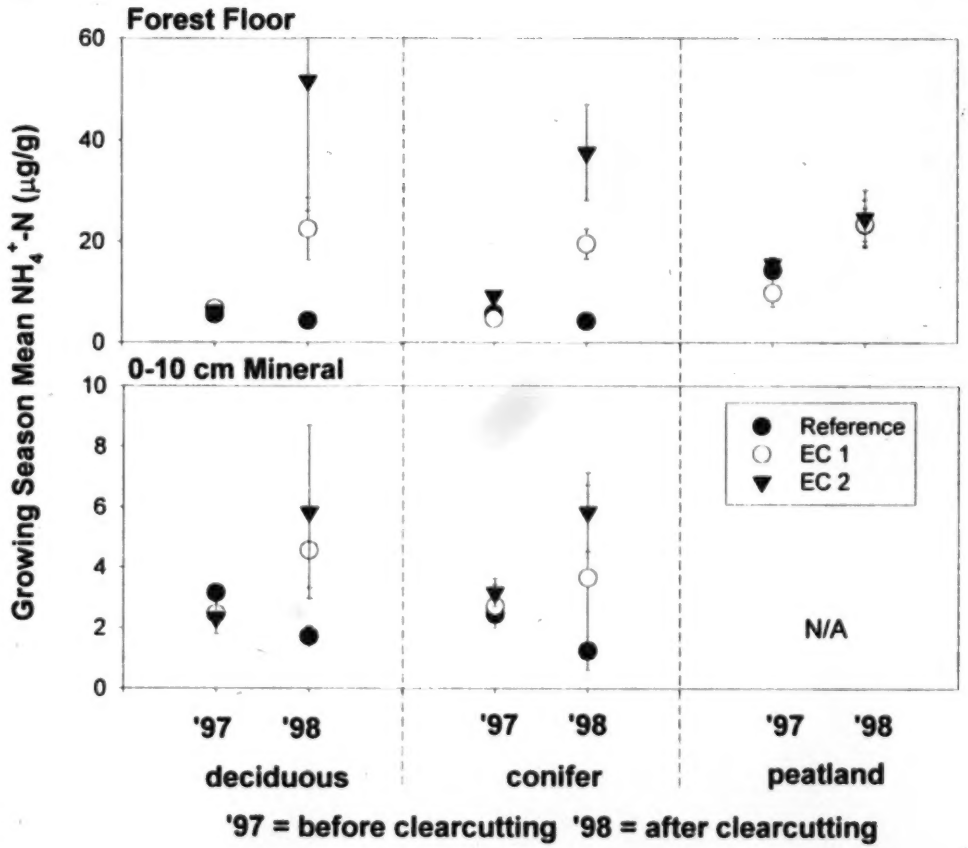

Figure 2-4: Growing season mean (± SE) NH_4^+-N for forest floor and 0-10 cm mineral soils within deciduous, conifer and peatland forest types for 1997 (pre-logging) and 1998 (post-logging).

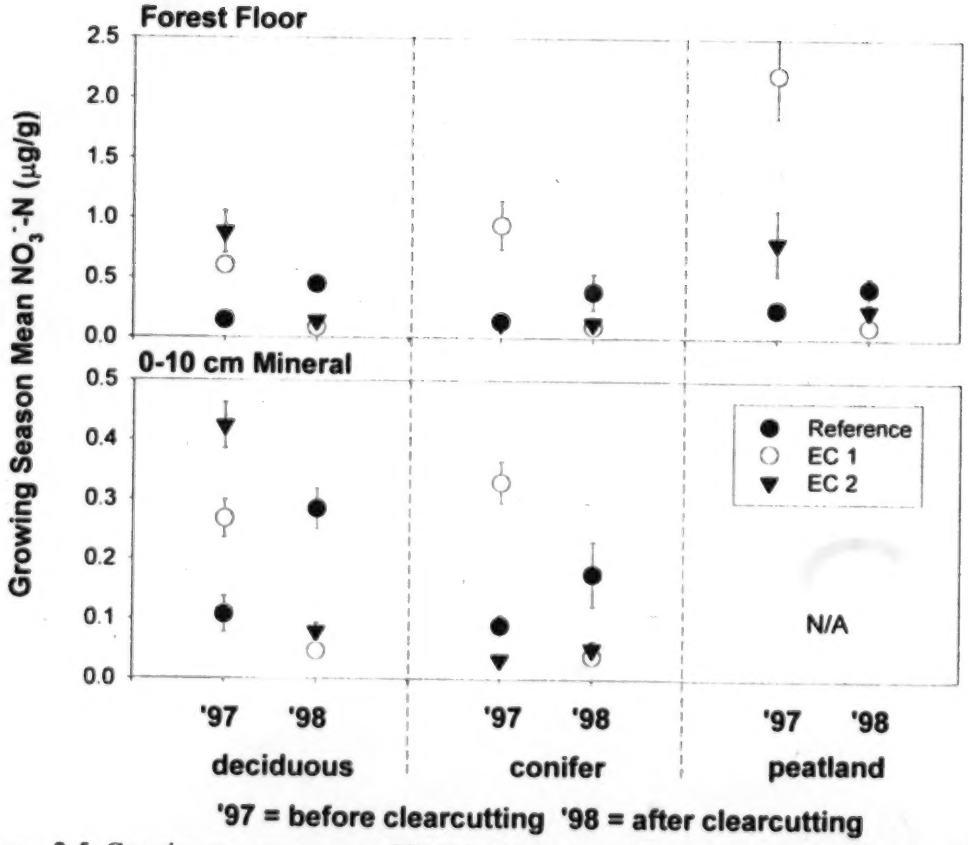

Figure 2-5: Growing season mean (± SE) NO_3^--N for forest floor and 0-10 cm mineral soils within deciduous, conifer and peatland forest types for 1997 (pre-logging) and 1998 (post-logging).

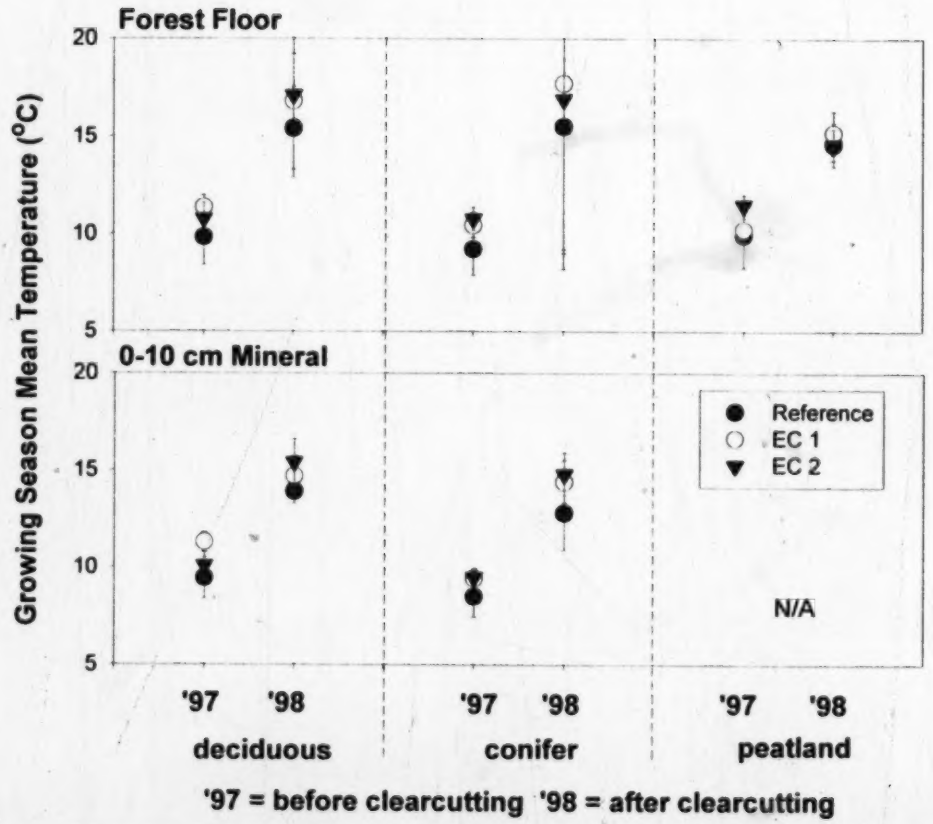

Figure 2-6: Growing season mean (± SE) soil temperature for forest floor and 0-10 cm mineral soils within deciduous, conifer and peatland forest types for 1997 (pre-logging) and 1998 (post-logging).

found using 1997 data. There was a tendency for both the reference forest floor and 0-10 cm mineral soils in the upland stands to have higher mineralization rates in 1998 compared to 1997 (Table 2-2). Mineralization rates were as high in forest floor soils in 1998 compared to 1997 in EC1 and in the EC2 conifer stand, but there was a major drop in the rate of mineralization in the EC2 deciduous stand. For 0-10 cm mineral soils, mineralization rates in the reference conifer and deciduous stand were slightly higher in 1998 compared to 1997, while a decrease in mineralization rates were measured in both forest types in the two experimental catchments. However, the 1998 mineralization rates were similar to those measured in 1996. In both years, mineralization rates in the reference peatland were ten times higher than in the experimental peatlands, and rates were similar between years within each catchment.

Growing season total nitrification rates for forest floor and 0-10 cm mineral soils in the reference deciduous and conifer stands were 2-4 μg/g and 0.8-1 μg/g, respectively, higher in 1998 compared to 1997 (Table 2-2). This coincided with 3-7°C higher growing season mean soil temperatures (Figure 2-7). However, 1998 nitrification rates were similar to 1996 values. Despite significantly higher temperatures, soils were not drier in 1998 in any of the forest types or catchments (Figure 2-7). Nitrification rates in the deciduous and conifer stands of the 2 experimental catchments were similar between years despite higher soil temperatures in 1998. Although peatland temperatures were 4-5°C higher in 1998, nitrification rates were near zero in both 1997 and 1998. Negligible nitrification rates in the peatlands coincided with high soil moisture, >32 %, in both years (Figure 2-7).

There were clear differences in growing season mean NH_4^+-N between the reference and experimental catchment in the three forest types, at both depth increments (Figure 2-4). In the reference catchment, NH_4^+-N in the conifer and deciduous stands was slightly lower in 1998 compared to 1997. In contrast, NH_4^+-N in forest floor soil of the deciduous and conifer stands in the experimental catchments increased by 14-45 μg/g and 12-31 μg/g, respectively, in 1998, although within-catchment variation was large. Ammonium availability in all peatland stands increased by 10-12 μg/g from 1997 to 1998.

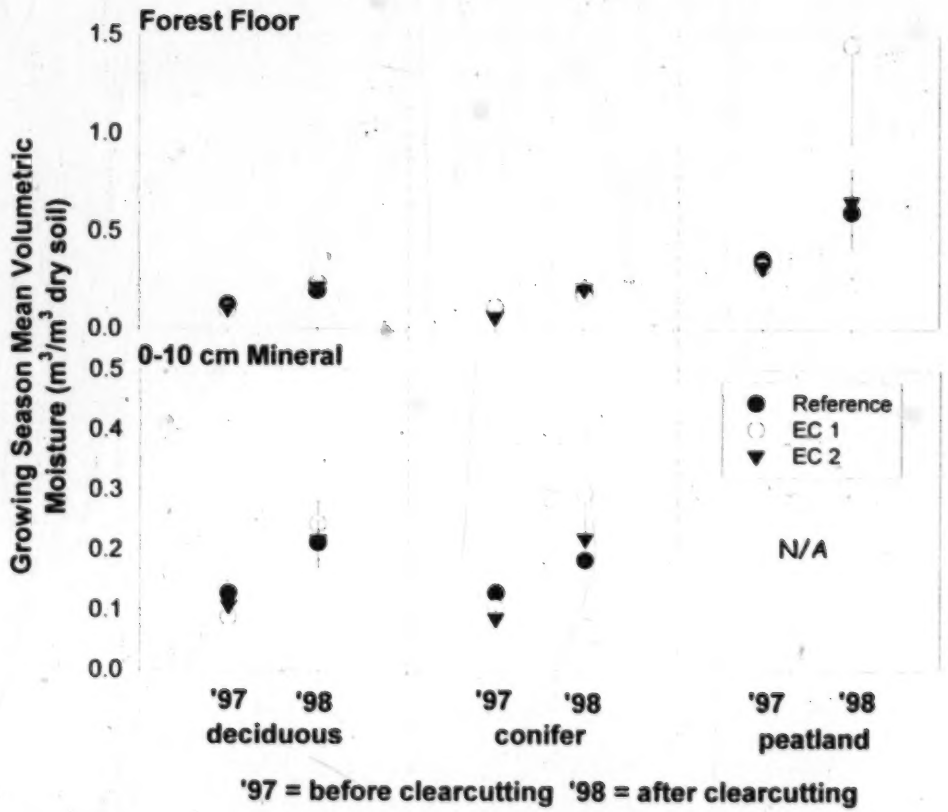

Figure 2-7: Growing season mean (± SE) volumetric soil moisture for forest floor and 0-10 cm mineral soils within deciduous, conifer and peatland forest types for 1997 (pre-logging) and 1998 (post-logging).

Marked differences between years in growing season mean NO_3^--N was observed in all stands (Figure 2-5). Nitrate availability was significantly higher in the reference stand in all three forest types and at both soil depths in 1998 compared to 1997 ($P < 0.05$). In contrast, NO_3^--N in 1998 was 0.2-2.0 μg/g lower in the experimental catchments within all forest types.

Mean TDN availability and mobilization rates were similar in June and September 1998 ($P > 0.10$), thus the dates were combined to give an estimate of DON mobilization rates during the first year after logging (Figure 2-8). Total dissolved N was 10 to 25 times higher than inorganic N in both uncut reference and logged soils. Total dissolved N was highest in the peatlands, intermediate in the conifer forest floor soils and lowest in the conifer mineral soils. No clear differences in TDN mobilization were observed between uncut reference and logged soils in either the peatland or conifer stands.

2.4.3 Reciprocal Transplants

June and August 1997 soil temperatures were 4-7 °C and 12-14 °C higher in the logged forest floor and mineral soils, respectively, compared to the uncut soils (Table 2-4). The mineral soil in the logged stand (along the skidder trail) had 11 % lower moisture in June 1997 compared to the uncut stand (Table 2-4). However, no other differences in soil moisture were noted among the logged and uncut stands. Reciprocal transplant experiments conducted on conifer soils in June 1997 revealed a trend of higher mineralization rates in logged sites compared to uncut sites, although the results were not significant (Table 2-4). A general increase in mineralization rates was measured when uncut soils were transplanted to the cut and a general decrease in mineralization rates was measured when cut soils were transplanted to the uncut. However, the results were not significant. Nitrification was not detected on either date in lower or higher temperature soils (Table 2-4). The low rates, low sample size and relatively high variability contributes to the lack of significant differences between sites.

Transplant experiments were conducted in peatland and conifer (forest floor and 0-10 cm mineral) stands in August 1998 with a larger sample size (Table 2-5). Similar to

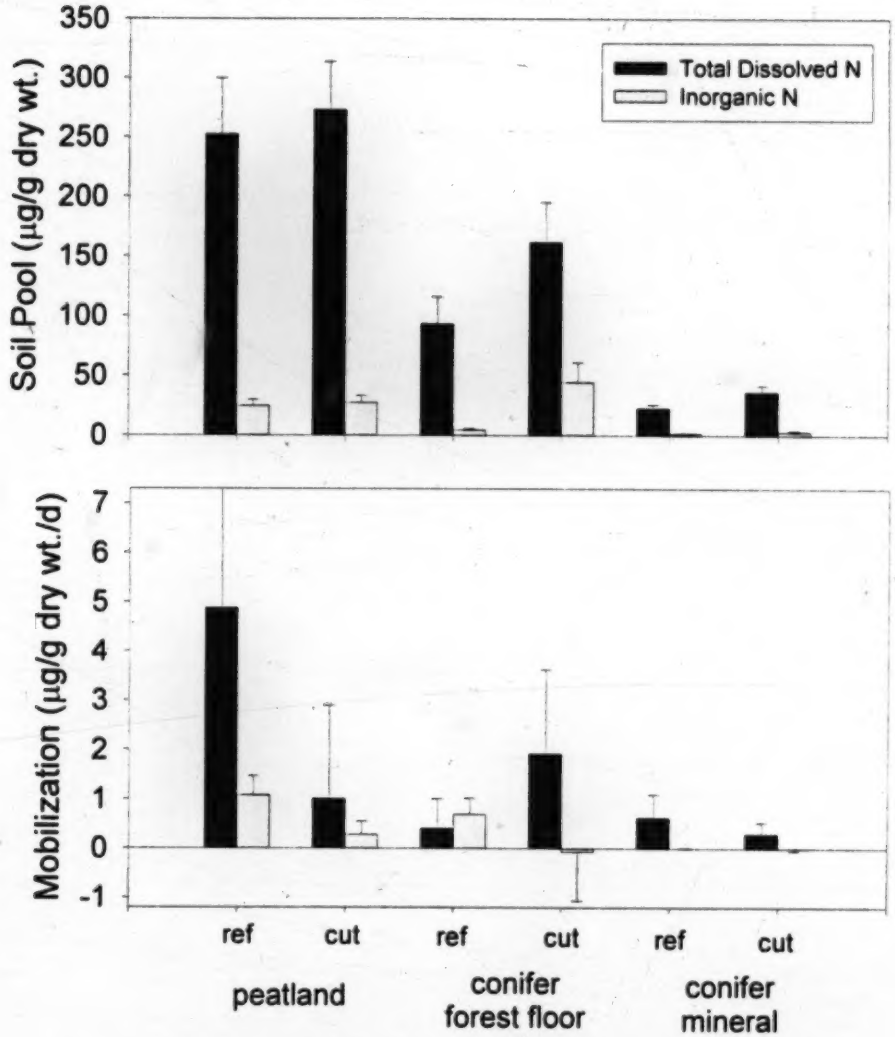

Figure 2-8: Mean (± SE) soil N (top) and mobilization (bottom) of total inorganic N and total dissolved N (TDN). The difference between TDN and TIN is dissolved organic N (DON).

Table 2-4: Net mineralization, nitrification, temperature and moisture for conifer undisturbed and cut soil incubated in their own location of origin and transplanted in the other area in Jun and Aug 1997. Values are mean (±SE), n = 5. T-tests with Bonferroni adjusted probabilities for multiple comparisons were used to test the various null hypotheses.

ORIGINAL LOCATION: INCUBATED IN:		Uncut Uncut (U-U)	Uncut Cut (U-C)	Cut Uncut (C-U)	Cut Cut (C-C)	p-values for tests of null hypotheses: U-U=U-C	C-U=C-C	U-U=C-U	C-C=U-C	U-U=C-C
N Mineralization (µg/g soil/d)										
forest floor	June	0.10 (0.03)	0.12 (0.00)	0.08 (0.02)	0.21 (0.10)	1.000	1.000	1.000	1.000	0.329
	September	1.48 (0.81)	0.32 (0.12)	0.16 (0.01)	0.30 (0.11)	1.000	0.838	0.571	1.000	0.185
mineral/skidder trail	June	0.10 (0.03)	0.85 (0.25)	-0.03 (0.00)	0.13 (0.10)	0.120	0.746	0.068	0.170	0.808
	September	-0.03 (0.14)	-0.10 (0.02)	0.01 (0.02)	0.63 (0.68)	1.000	1.000	1.000	1.000	0.370
Nitrification (µg/g soil/d)										
forest floor	June	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)	0.03 (0.00)	1.000	1.000	1.000	1.000	0.376
	September	0.00 (0.00)	0.00 (0.00)	0.02 (0.00)	-0.01 (0.00)	1.000	1.000	1.000	0.227	0.228
mineral/skidder trail	June	0.00 (0.00)	0.02 (0.00)	0.00 (0.00)	0.01 (0.00)	0.702	0.258	1.000	1.000	0.400
	September	-0.01 (0.00)	0.00 (0.00)	-0.01 (0.00)	-0.01 (0.00)	0.972	1.000	1.000	0.998	0.986
Soil Temperature (°C)										
forest floor	June	9.0 (0.5)	ND	ND	16.3 (0.6)	NA	NA	NA	NA	<0.001
	September	13.5 (0.2)	ND	ND	18.2 (1.0)	NA	NA	NA	NA	0.002
mineral/skidder trail	June	7.9 (0.2)	ND	ND	19.6 (1.1)	NA	NA	NA	NA	<0.001
	September	12.8 (0.3)	ND	ND	26.4 (0.6)	NA	NA	NA	NA	<0.001
Volumetric Soil Moisture (m^3/m^3)										
forest floor	June	51.1 (4.1)	ND	ND	29.5 (1.7)	NA	NA	NA	NA	0.007
	September	31.6 (4.6)	ND	ND	35.6 (3.4)	NA	NA	NA	NA	1.000
mineral/skidder trail	June	23.0 (2.7)	ND	ND	22.3 (7.9)	NA	NA	NA	NA	0.129
	September	24.8 (6.3)	ND	ND	29.0 (5.8)	NA	NA	NA	NA	1.000

Note: ND, no data; NA, not applicable.

Table 2-5: Net mineralization, nitrification, moisture and temperature for peatland and conifer uncut and cut soil incubated in their own location and transplanted in the other area, Aug 1998 (EC1 soil). Values are mean (±SE), n = 10. T-tests with Bonferroni adjusted probabilities for multiple comparisons were used to test the various null hypotheses.

ORIGINAL LOCATION: / INCUBATED IN:		Uncut / Uncut (U-U)	Uncut / Cut (U-C)	Cut / Uncut (C-U)	Cut / Cut (C-C)	p-values for tests of null hypotheses: U-U=U-C	C-U=C-C	U-U=C-U	C-C=U-C	U-U=C-C
N Mineralization (ug/g soil/d)										
Peatland	0-10 cm	-0.06 (0.05)	2.94 (1.41)	1.16 (0.66)	1.02 (0.43)	0.060	0.861	0.392	0.927	0.029
Conifer	forest floor	-0.02 (0.06)	0.74 (0.55)	1.45 (0.85)	1.82 (1.00)	0.217	0.792	0.481	1.000	0.100
	0-10 cm mineral	-0.01 (0.04)	-0.06 (0.02)	0.06 (0.09)	-0.00 (0.06)	0.401	0.582	1.000	1.000	0.911
Nitrification (ug/g soil/d)										
Peatland	0-10 cm	0.01 (0.00)	0.09 (0.02)	0.00 (0.00)	-0.00 (0.00)	0.003	0.756	0.059	0.002	0.003
Conifer	forest floor	0.04 (0.02)	0.01 (0.01)	0.03 (0.00)	0.03 (0.01)	0.141	0.762	1.000	0.215	0.594
	0-10 cm mineral	0.02 (0.01)	0.01 (0.00)	0.02 (0.00)	0.02 (0.00)	0.154	0.565	1.000	0.332	0.707
Soil Temperature (°C)										
Peatland	0-10 cm	14.0 (0.2)	ND	ND	16.6 (0.2)	NA	NA	NA	NA	<0.001
Conifer	forest floor	15.4 (0.3)	ND	ND	17.6 (0.2)	NA	NA	NA	NA	<0.001
	0-10 cm mineral	12.8 (0.1)	ND	ND	15.6 (0.1)	NA	NA	NA	NA	<0.001
Volumetic Moisture (m^3/m^3)										
Peatland	0-10 cm	0.16 (0.03)	ND	ND	0.37 (0.02)	NA	NA	NA	NA	<0.001
Conifer	forest floor	0.06 (0.01)	ND	ND	0.14 (0.02)	NA	NA	NA	NA	<0.001
	0-10 cm mineral	0.09 (0.01)	ND	ND	0.17 (0.02)	NA	NA	NA	NA	<0.001

Note: ND, no data; NA, not applicable.

1997, conifer forest floor and 0-10 cm mineral soils in the cut stand were 2-3 °C warmer than uncut soils ($P < 0.001$). Moisture was significantly higher in the logged stand compared to the uncut stand at both soil depths (Table 2-5). Despite higher temperatures in the conifer forest floor and 0-10 cm mineral logged soils, transplanting of soil to a different temperature had no effect on mineralization and nitrification rates.

The logged peatland had significantly higher temperature (2.6 °C) and 19 % higher moisture than the uncut peatland (Table 2-5). Mineralization rates were significantly higher in the logged peatland while nitrification rates were significantly higher in the uncut peatland (Table 2-5). Peatland soils taken from the uncut site and incubated in the higher temperature logged site had significantly greater mineralization and nitrification rates than the same soils incubated in the uncut site.

2.4.4 Conifer Regeneration Study

In all but the 0 and 64 yr regenerating stands, growing season mean soil temperatures were 3-5 °C higher in the logged stands than the uncut stands in both forest floor and 0-10 cm mineral soils (Figure 2-9). The largest difference (5 °C) was noted in the 2 yr regenerating stand.

Growing season mean forest floor soil moisture ranged between 9 and 18 % in the uncut stands and between 5 and 20 % in the regenerating stands (Figure 2-9). Furthermore, moisture was similar among uncut and younger regenerating stands, but significantly lower in the 64 yr regenerating stand compared to the paired uncut stand ($P < 0.001$). For 0-10 cm mineral soils, growing season mean moisture for all stands ranged from 5 to 23 %, with no consistent trend between regenerating and uncut stands. Moisture was 4 % lower in the 64 yr regenerating stand compared to the paired uncut stand ($P = 0.03$), although the sand in the regenerating stand was visually coarser than that in the uncut stand.

Growing season mineralization rates in the forest floor ranged between 31 to 47 μg/g in the uncut and 10 to 35 μg/g in the regenerating stands (Figure 2-10), falling

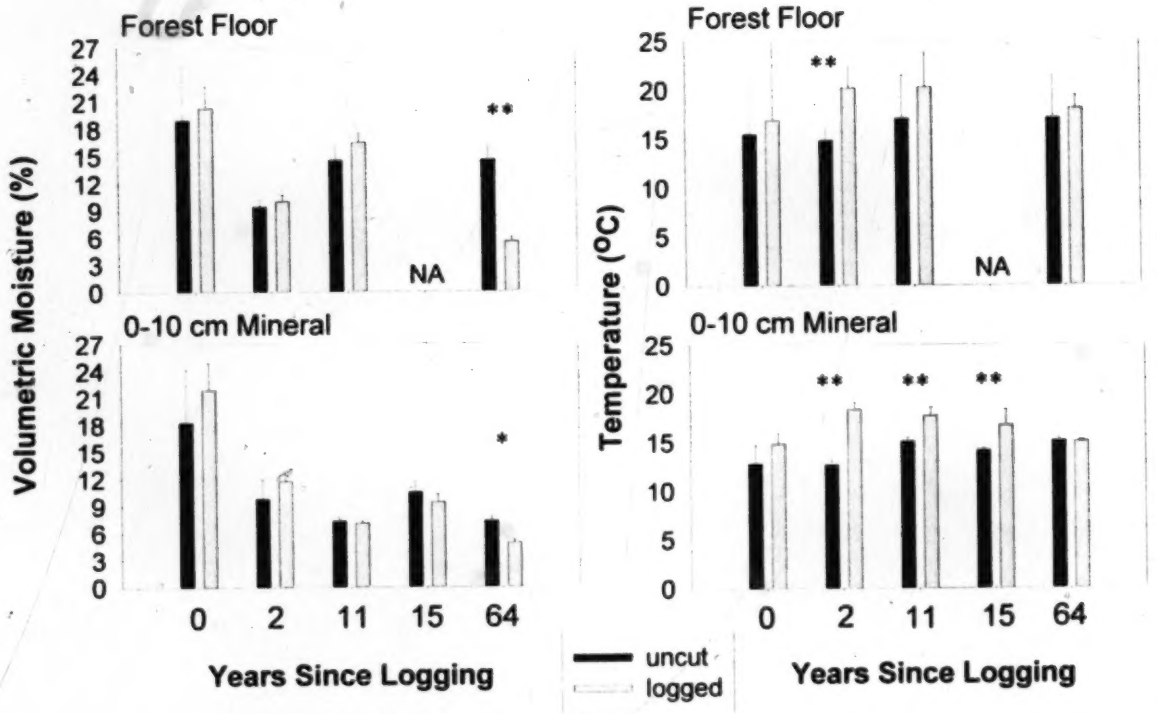

Figure 2-9: Growing season mean volumetric soil moisture and temperature for forest floor and 0-10 cm mineral soils. Bars represent 1 SE, n = 7. NA = no soil layer present at logged site. * = significant difference between uncut and regenerating soil at $P \leq 0.05$, ** = significance at $P \leq 0.001$.

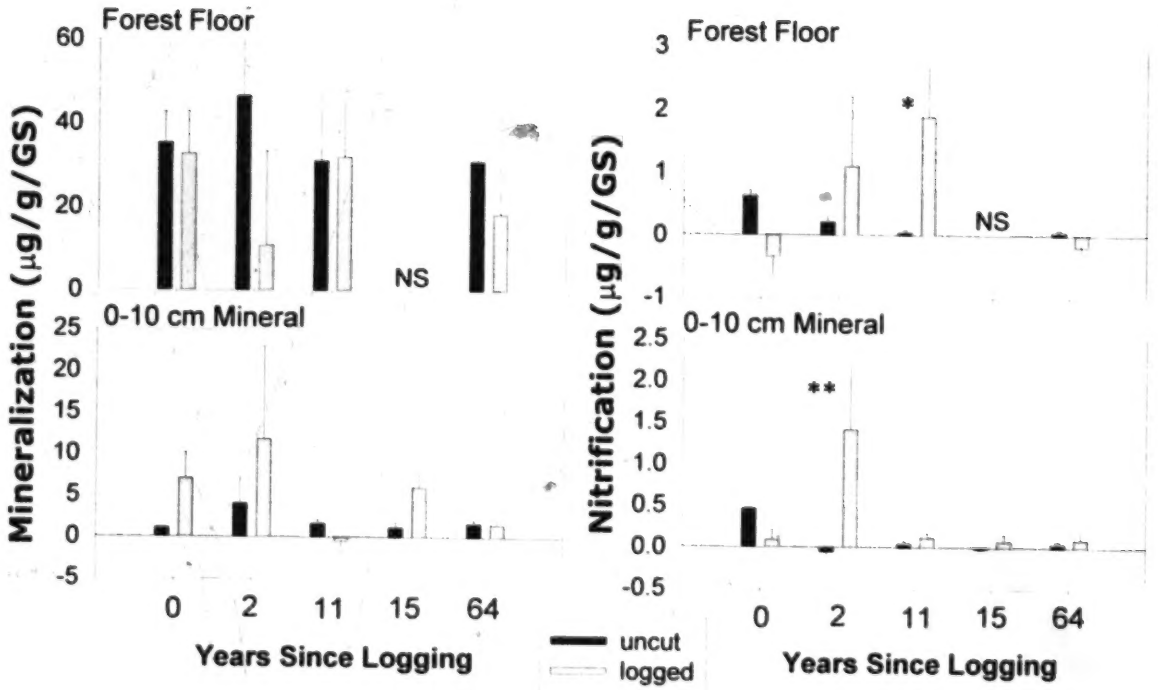

Figure 2-10: Growing season total net mineralization and nitrification for forest floor and 0-10 cm mineral soils. Bars represent 1 SE, n = 7. NA = no soil layer present at logged site. * = significant difference between uncut and regenerating soil at $P \leq 0.05$, ** = significance at $P \leq 0.001$.

within the range of mineralization rates measured in the conifer stands within the 3 catchments (Table 2-2). Mineralization rates in the 0-10 cm mineral uncut and regenerating stands ranged between 1 and 11 μg/g (Figure 2-10). No significant differences in mineralization rates between the uncut and different age regenerating stands were found at either soil depth.

Nitrification rates for the growing season were similar in both forest floor and 0-10 cm mineral soils, ranging from –0.1 to 0.2 μg/g in the uncut stands and from –0.2 to 1.9 μg/g in the regenerating stands (Figure 2-10). Regression analyses revealed no correlation for nitrification rates in forest floor soils of the various uncut stands ($P = 0.13$) or different age regenerating stands ($P = 0.13$). Although forest floor soils in both the 2 yr and 11 yr regenerating stands had 0.9-1.9 μg/g higher nitrification rates than their respective uncut stands, increases were significant only in the 11 yr age class ($P = 0.01$). Analysis of variance and subsequent contrasts within each aged stand in 0-10 cm mineral soils show nitrification rates in the 2 yr regenerating stand were significantly higher than in its paired uncut stand ($P < 0.001$), but this trend was not observed in older regenerating stands.

Soil NH_4^+-N in all the uncut sites was 6-7 μg/g and 1.0-1.4 μg/g for the forest floor and 0-10 cm mineral soils, respectively (Figure 2-11). Forest floor NH_4^+-N was significantly higher in the 2 yr regenerating stand compared to the 2 yr uncut stand ($P = 0.04$). In the 0-10 cm mineral soils, NH_4^+-N was about 1 μg/g higher in the 2 yr ($P = 0.01$) and 11 yr ($P = 0.02$) regenerating stands compared to their paired uncut stands. Nitrate availability in the uncut stands was similar in forest floor and 0-10 cm mineral soils, ranging between 0.03 and 0.13 μg/g (Figure 2-11). Soil NO_3^--N for the forest floor and 0-10 cm mineral soils in the regenerating stands were similar to that in the uncut stands.

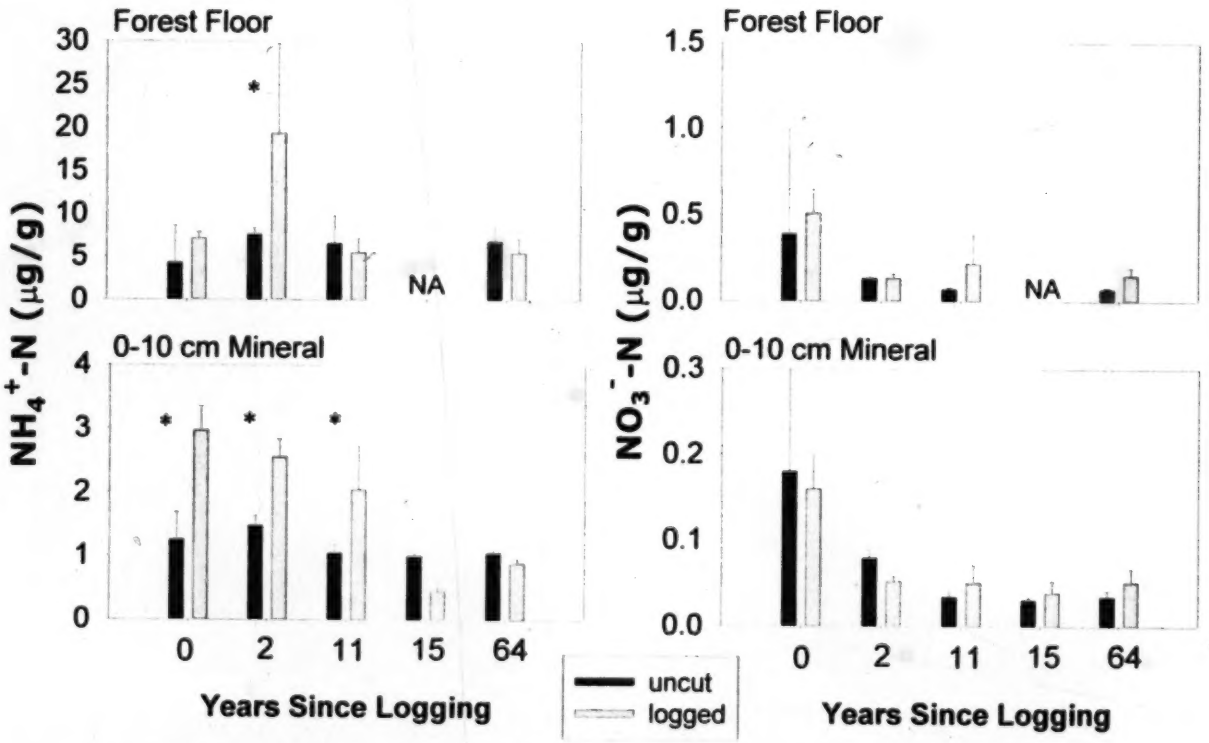

Figure 2-11: Growing season mean NH_4^+-N and NO_3^--N for forest floor and 0-10 cm mineral soils. Bars represent 1 SE, n = 7. NA = no soil layer present at logged site. * = significant difference between uncut and regenerating soil at $P \leq 0.05$, ** = significance at $P \leq 0.001$.

2.5 Discussion

2.5.1 Pre-Cut Conditions

Nitrogen mineralization rates in 1997 were low and did not differ among uncut upland deciduous and conifer stands. This is inconsistent with most other studies, where higher net mineralization rates have been found in deciduous stands compared to conifer stands and peatlands (e.g. Hill and Shackleton 1989; Chapin 1996). In the above mentioned studies, differences in net mineralization rates among forest types are related to differing C/N ratios, moisture and soil N. Similar soil C and N content, pH, moisture and temperature were measured for the deciduous and conifer stands in this study and may contribute to the lack of difference in mineralization rates among upland stands. Also, differences in mineralization rates among upland forest types may not exist in this system, even if soil characteristics differed, as low substrate availability likely limits mineralization rates. Thus the lack of difference in mineralization rates among forest types in this system may reflect the low rates.

Many studies have shown that peatlands have lower rates of net mineralization than conifer and deciduous stands (e.g. Hill and Skackleton 1989; Zak and Grigal 1991), however comparable net mineralization rates were measured for peatlands and conifer stands in this study. The presence of alder species in peatlands may promote mineralization due to higher soil organic N (Ohrui et al. 1999). This is not likely to influence mineralization rates of the peatlands in this study as the ones that contained 5-23 % alder did not have higher mineralization rates than those without alder. Similar net mineralization rates in peatlands and conifer stands here may be the result of different mechanisms operating in these forest types. Jonasson and Shaver (1999) suggest low net rates in peatlands are likely due to reduced or absent immobilization of N in peatlands and slow rates of N production. High immobilization rates in conifer soils have been shown to result in low net rates (Stark and Hart 1997). Gross rates of N production and immobilization in the conifer and peatland soils will be explored in chapter 3 of this thesis. If this were the case, then the potential exists for net NO_3^- production in peatlands

during periods of water table draw down (Williams 1974) and subsequent export of NO_3^- to streams and lakes.

Growing season total net mineralization rates of –2.9-10 kg/ha in upland deciduous and conifer stands of this region are among the lowest rates previously recorded for arctic, boreal and temperate forest soils (as reviewed by Binkley and Hart 1989). Upland net mineralization rates fall within the range of those measured in conifer stands within the same region at the Experimental Lakes Area (ELA) (4-6 kg/ha/y: Lamontagne 1998). They are slightly lower than those measured in upland stands at Isle Royale (11-14 kg/ha/yr: Stottlemyer et al. 1995), pine tundra soils in Colorado (10-12 kg/ha/yr: Fisk and Schmidt 1995) and about 50% lower than in three Boreal Mixed-wood stands (11-30 kg/ha/yr: Carmosini 2000). Peatland growing season mineralization rates for my study catchments, 0-4 kg/ha, are within the same range as those measured in a southern Ontario riparian hemlock stand (3.3 kg/ha/yr: Hill and Shackleton 1989). Mineralization rates are slightly lower than rates measured for fens in Alberta (5.9 kg/ha/yr: Mewhort 2000) and 75 % lower than net mineralization rates measured for deciduous swamps in Minnesota and in hemlock-fir dominated peatlands in central Ontario (15-19 kg/ha/yr: Zak and Grigal 1991; Devito et al. 1999). The mineralization rates are up to an order of magnitude lower than in Swedish bogs (8-51 kg/ha/yr: Urban and Eisenreich 1988).

No clear changes in soil nitrification rates with respect to forest types were observed in this study. However, large contrasts in nitrification between undisturbed conifer, deciduous and peatland stands have been widely reported in other forests due to differing C/N ratios, pH, the recalcitrant nature of conifer litter, and higher polyphenols in conifer soils (Olson and Reiners 1983; Hill and Shackleton 1989; Zak and Grigal 1991; Stottlemyer et al. 1995; Devito et al. 1999). The form of N available to the trees may be an important determinant of patterns in soil N dynamics in both temperate and boreal forests (Min et al. 1999). In a boreal system, such as the Coldwater Lakes study area, where the soil N pool is dominated by NH_4^+, little difference in nitrification rates between landscape units would be expected. Fertilization experiments have shown that net nitrification is controlled by NH_4^+ availability (Robertson 1982). Consequently, low

substrate availability may limit nitrification in each forest type. Coupled with this, conifer and deciduous stands, with C/N ratios of 25-38 and 27-59, respectively, suggest net immobilization of NO_3^- in the upland forest soils. The potential for net NO_3^- production in the study peatlands is likely limited by the anoxic conditions usually associated with high soil moisture and water tables. The exceedingly low net nitrification rates seen in this study coupled with relatively high within-stand variation likely contributed to difficulties in detecting differences in nitrification rates among forest types.

Growing season nitrification rates of –0.2-0.8 kg/ha for upland forest stands are similar to stands within the same region at the ELA (Lamontagne 1998), but are generally lower than those measured in most other boreal, temperate and alpine tundra forests (Binkley and Hart 1989; Foster 1989; Hill and Shackleton 1989; Fisk and Schmidt 1995; Chapin 1996; Devito et al. 1999; Ohrui et al. 1999). Peatland growing season nitrification rates at my study site (<0.2 kg/ha) were slightly lower than nitrification rates found in minerotrophic fens in central Alberta (0.17-0.89 kg/ha/54 d: Humphrey and Pluth 1996), in two hemlock-fir peatlands in central Ontario (-0.5-0.5 kg/ha/yr: Devito et al. 1999) and much lower than nitrification rates measured in a southern Ontario riparian cedar and hemlock stand (3.4 kg/ha/yr: Hill and Shackleton 1989). There appears to be limited potential for N leaching from the Coldwater Lakes soils due to low net production rates of mobile forms of N and poor soil quality.

2.5.2 Uncut vs. Logged Uplands

There was a pronounced increase in conifer and deciduous upland NH_4^+ of the two experimental catchments compared to the reference catchment and the pre-cut years, although no increase in net mineralization rates were observed. Soil NO_3^- was not higher after logging of the experimental catchments. Greater availability of N in clearcuts is often attributed to higher decomposition of organic matter as a result of increased soil temperature and moisture (Adams and Attiwill 1991; Prescott 1997) and a reduction in plant N demand. It is unlikely that the higher NH_4^+ in the experimental catchments resulted from increased decomposition of conifer litter and logging residues as it takes a

considerable amount time to release this N (Berg and Staaf 1981; Lundgren 1982) and increased net mineralization rates were not observed. Higher soil NH_4^+ content immediately after clearcutting may be a result of bacterial and fungal death representing a larger fraction of the available N pool (Hendrickson et al. 1985) or simply to reduced plant uptake. Olson and Reiners (1983) showed higher NH_4^+ but not NO_3^- in N-poor subalpine Balsam fir soils when plant uptake was prevented. Continued higher soil N during the first year after harvesting is generally attributed to decomposition of fine roots severed during clearcutting (Lundgren 1982). However, higher NH_4^+ was found in the 0yr, 2 yr and 11 yr regenerating stands compared to the uncut reference stands in the regeneration study, without a coincident increase in net mineralization rates. These results suggest that plant uptake of NH_4^+ may have been reduced for a short period following clearcutting, allowing NH_4^+ to accumulate. Subsequent regeneration and an increase in plant uptake of N by seedlings and ferns likely occurred at a rate equal to or less than that in uncut areas.

Total dissolved N was 10 to 25 times higher than TIN, showing the dominance of DON in the N pool of the peatland and conifer soils. Contrary to expectation, soil DON in conifer stands and peatlands was not higher in logged stands during the first growing season after clearcutting relative to uncut stands. This contrasts with the findings of Neiminen (1998) who measured two to threefold increases in soil DON, depending on the presence of slash, immediately after logging boreal peatlands in southern Finland. No differences in soil DON between uncut and logged conifer and peatland forest soils suggests that plants are likely not relying on DON as a source of N nutrition. However, problems with disturbance during sampling of the uncut soils may complicate the lack of a clear trend in soil DON with logging. Root disturbance during soil sampling can elevate DON concentrations (Lamontagne 1998), potentially artificially elevating DON estimates in the uncut sites.

The rates of TDN mobilization were similar to TIN mobilization rates, indicating DON mobilization rates were small in these soils. DON mobilization rates measured in the conifer stands were within the range of those in similar conifer stands at the ELA (Lamontagne 1998), and suggest a low potential for leaching loss from these sites.

However, there is some evidence for increased DON export from the experimental catchments during the first growing season after logging (C. Allan, unpubl. data). However, it is not yet clear if this is due to higher water yields from the experimentally logged catchments compared to the reference catchment.

The catchment data show that temperature in 1998 was 3-7 °C higher in all forest types, suggesting that if N transformation rates are at least partly regulated by temperature, rates should have been higher in 1998 than in 1997. Likewise, temperatures in the 2, 11 and 15 yr regenerating conifer stands were 4-7 °C higher than in the uncut stands. Higher temperatures have been previously shown to stimulate nitrification in both lab experiments and field studies (Mahli and McGill 1982; Devito et al. 1999; Wilson et al. 1999). Increased temperatures in 1998 compared to 1997, particularly due to a negligible snowpack during the spring, were associated with higher nitrification rates in both the conifer and deciduous stands of the reference catchment. The conifer and deciduous forest types of the experimental catchments should have had comparable increases in nitrification rates to the reference stands due to similar increases in soil temperatures in 1998. However, the clearcut stands in the two experimental catchments had the same rates of nitrification in both years. This coupled with slightly lower soil NO_3^- and high C/N ratios in the clearcut stands suggests that the immediate response to clearcutting was an increase in NO_3^- immobilization leading to lower net nitrification rates. Stimulation of NO_3^- immobilization immediately following clearcutting may be a result of severed roots leaking photosynthetically derived labile C, possibly relieving C limitations.

It was expected that nitrification rates would be unaffected by clearcutting in the deciduous (primarily aspen) stands. Studies in other aspen forests have found that leaching loss and disruption of N dynamics after clearcutting are negligible (Silkworth and Grigal 1982; Alban and Perala 1990) due to aspen's high N demands (Richardson and Lund 1975). However, reduced net nitrification rates and a statistically significant reduction in soil NO_3^- were observed in the clearcut aspen soils in my study. Lower net nitrification is likely not attributed to altered C/N ratios, as only small decreases in C/N ratios were found after logging. Hence, the reason for this uncharacteristic response of the

aspen stands to clearcutting is unclear. Slightly lower soil NO_3^- may be attributed to high uptake by regenerating aspen sucklings (Richardson and Lund 1975; Alban and Perala 1990).

Although fertilization experiments have shown that nitrification is controlled by NH_4^+ availability (Robertson 1982), there was no immediate stimulation of nitrification rates to the higher soil NH_4^+ in the catchments in my study. Higher NH_4^+ and nitrification rates in the 2 yr and 11 yr clearcut stands of the regeneration chronosequence study suggest that it may take more time for the nitrifier population to respond to increased NH_4^+ availability. Delayed nitrification after clearcutting has been found by Vitousek et al. (1982), even though ammonification was immediately enhanced. Hendrickson et al. (1985) found no change in nitrifier populations or nitrification rates during the first year following clearcutting of a sandy glacial till site in the Ottawa Valley. Both studies suggest a delay in nitrification as the reason. In contrast, microbial biomass and nitrification were found to increase within the first year after clearcutting in a Norway spruce stand, southeastern Finland (Langkramer and Lettl 1983). Other studies in boreal coniferous stands have found detectable nitrification two or more years following clearcutting (e.g. Munson and Timmer 1995; Paavolainen and Smolander 1998), but no measurements were made during the first growing season in these studies.

The presence of a lag before nitrification is stimulated following clearcutting has only been documented at a few sites, although several mechanisms may delay nitrification. Low nitrification at my sites may be attributed to small pre-harvest nitrifier populations and little increase in population size within the first growing season due to similar organic N observed in logged and uncut soils. Enhanced nitrification in the 2 yr and 11 yr clearcuts suggest higher nitrifier populations, increased nitrifier activity or a reduction in microbial NO_3^- immobilization due to soil labile C depletion over time (Prescott 1997). Alternatively, pre-harvest nitrifier populations may have been mostly comprised of autotrophic nitrifiers. Clearcutting has been shown to shift the dominant nitrifiers from autotrophic to heterotrophic (Sollins and McCorison 1981). Other potential contributors to delayed nitrification include soil pH < 4.0, P deficiency and

allelochemical inhibition by high phenolic concentrations in conifer residues (Oldson and Reiners 1983; Persson and Wiren 1995; Janssen 1996; Paavolainen and Smolander 1998).

Although net nitrification rates were increased in the 2 yr and 11 yr regenerating conifer stands, soil NO_3^- did not increase. This suggests that the NO_3^- is (i) undergoing dissimilatory nitrate reduction, or (ii) being lost from the soil through leaching or plant uptake. Further studies are needed to assess the importance of dissimilatory nitrate reduction in maintaining low soil NO_3^- despite elevated nitrification in clearcut conifer stands. Loss of NO_3^- from this system could potentially occur through flushing from the soil during rain events. However if this were the case, a characteristic pattern of high available NO_3^- after relatively long dry periods and low availability after rainfall may be observed. Despite the low soil moisture content throughout the study period, no seasonal increases in NO_3^- were observed (data not shown). As this system is a low N system, soil NO_3^- is negligible despite enhanced nitrification. The vegetation may also take up excess nitrate, however, recent studies have shown that conifer trees discriminate against soil NO_3^- (Kronzucker et al. 1997). Soil NO_3^- uptake is likely limited in the 2 yr and 11 yr regenerating conifer stands as jack pine dominates.

The data suggest that clearcutting increases the availability of NH_4^+ and enhances nitrification rates, after a 1-2 yr time lag, for up to 11 yrs in conifer soil of this region. The magnitude of the nitrification increase observed here is similar to that observed in other N-poor systems (reviewed by Lundborg 1997), but very small compared to that in other clearcut ecosystems (Mladenoff 1987; Carmosini 2000). Frazer et al. (1990) reported similar results; enhanced nitrification in 5 and 17 yr old regenerated clearcuts in a British Columbian pine dominated system. Few, if any, other long-term studies investigating effects of clearcutting on N dynamics have been conducted on the same forest stand or across a regeneration chronosequence at a number of different stands. Caution should be taken when applying these results to field management practices, as the clearcut stands were not replicated in my chronosequence study.

It has been previously thought that clearcutting increases net nitrification rates and soil NO_3^-, which may contribute to poor conifer regeneration in plantations (Montaginini et al. 1986) as conifers discriminate against NO_3^- (Lavoie et al. 1992;

Kronzucker et al. 1997). It is unlikely that high seedling failure is attributed to a logging-induced shortage of N for conifer regeneration at my study site as NH_4^+ was often higher in logged compared to uncut stands.

2.5.3 Uncut vs. Logged Peatlands

The transplant experiments revealed that logged peatland soils, with a 2.6 °C higher temperature and 20 % higher water content, had higher net mineralization rates and lower nitrification rates than uncut peatland soils. Additionally, uncut peatland soils incubated in the higher temperature peatland showed enhanced mineralization and nitrification rates. Enhanced mineralization rates found when uncut soil was incubated at a higher temperature may be due to increased cellulose decomposition. Trettin et al. (1997) recently found a positive correlation between temperature and cellulose decomposition in uncut peatlands. Higher mineralization rates in the logged peatland compared to the uncut peatland may be partially explained by higher soil temperatures in the logged peatland, however, there were large soil moisture differences between the peatlands. The higher net mineralization rates in the logged peatland compared to the unlogged peatland may be partially due to higher water content limiting nitrification rates (Hill and Shackleton 1989) and NH_4^+ immobilization by microorganisms.

In contrast to the reciprocal transplant study, mineralization and nitrification rates in the reference and experimental catchment peatlands were not different than in 1997, even though peat temperatures were ~6 °C higher in 1998 for all peatlands. Unlike the reduced soil moisture observed in the reciprocal transplant study, consistently high soil moisture (> 32 %) was measured in the reference and experimental peatlands during 1997 and 1998. This suggests that the interaction of temperature and moisture regime is important in enhancing mineralization rates in these peatlands. Low nitrification rates before and after logging are likely due to the restriction of nitrification by high soil moisture and water tables (Hill and Shackleton 1989) and acidic soil conditions (Chapin 1996). However, higher temperatures and lower soil moisture may not stimulate

decomposition, and thus N transformation rates, is microbial activity is more regulated by limiting nutrient conditions (Humphrey and Pluth 1996).

Growing season net mineralization and nitrification rates in the clearcut peatlands were not different than in the reference peatland within 4 months after clearcutting. Also, in 1997, mineralization rates were higher in the reference peatland compared to the experimental (uncut) peatlands. This difference was due to one month of high rates measured in the reference peatland (data not shown). Generally, monthly mineralization rates in the reference peatland were higher in 1998 compared to 1997. During 1997, the low experimental peatlands mineralization rates were due to low monthly rates, whereas in 1998, low rates were due to alternate months of negative and positive net mineralization rates, with the sum being near zero. Changes in N immobilization following clearcutting of peatlands will be explored in Chapter 3. More short and long-term research is needed on the controls of N transformations in clearcut peatlands, under a variety of hydrological conditions, to better understand the N dynamics and the potential for N retention post-harvest.

2.6 Conclusions

My results show net mineralization and nitrification rates do not differ among deciduous, conifer and peatland forest types in these low N content, headwater Boreal Shield catchments. Similar soil C and N content, pH, moisture and temperature measured for the deciduous and conifer stands in my study may contribute to the lack of difference in mineralization rates among upland stands. Similar nitrification rates among forest types are due to exceedingly low nitrification rates coupled with relatively high variation between catchments. Clearcutting does not appear to affect net mineralization rates in these forest types, regardless of forest type or age. However, soil NH_4^+ was higher immediately following logging in the conifer and deciduous upland stands, attributed to reduced plant uptake and senescent microbes. Reduced nitrification rates were noted in the conifer and deciduous upland soils during the first four months after clearcutting and enhanced nitrification rates were measured in 2 and 11 yr old regenerating conifer stands.

Peatland nitrification was not affected by clearcutting in the short-term, likely due to a combination of high water tables, low pH and limiting nutrient conditions, leading to high N immobilization. Additional research on a variety of forest types and ecosystems is needed to better predict the length and magnitude of effects of clearcutting on N availability and dynamics to ensure more successful tree regeneration and high N retention in upland and peatland forest soils.

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CHAPTER 3: HIGH NITROGEN IMMOBILIZATION FOLLOWING LOGGING IN CONIFER AND PEATLAND BOREAL FOREST SOILS

3.0 Introduction

The Boreal Shield landscape is characterized by a mosaic of peatlands and coniferous uplands. Thus, understanding N dynamics in both systems and their interactions are essential in understanding natural variability in N cycling and export and the impact of disturbance in the Boreal Forest. Acidic conifer forest soils, such as those in the Boreal Shield region, generally have negligible NO_3^- and relatively high NH_4^+. Likewise, the dominant form of inorganic N in peatlands is NH_4^+. The dominance of NH_4^+ in the inorganic N pool, coupled with recent studies on conifer nutritional requirements suggests that conifers discriminate against soil NO_3^- (Lavoie et al. 1992; Kronzucker et al. 1997). Field measurements of N transformations in undisturbed, boreal and arctic forest soils have shown negligible rates of net nitrification and relatively low rates of net N mineralization (Chapin 1996; Lamontagne 1998; Carmosini 2000). Similar results have been obtained in a temperate swamp (Hill and Shackleton 1989) and a few northern peatlands (Devito et al. 1999; Mewhort 2000; chapter 2). These data have led to the conclusion that NO_3^- has a relatively unimportant role in N dynamics of acidic boreal forest soils.

In ecosystems with high immobilization of nitrogen, however, net rates may be poor estimates of gross rates and thus underestimate the quantity of N passing through inorganic forms (Vitousek and Andariese 1986; Hart et al. 1994b). Recent work has demonstrated high gross rates of NO_3^- cycling in mature, temperate conifer forests (Davidson et al. 1992; Stark and Hart 1997; Stottlemyer and Toczydlowski 1999; Berntson and Aber 2000) and high gross rates of NH_4^+ cycling in one riparian fen bordering an agricultural field (Ambus et al. 1992). Despite these findings, the importance of N immobilization relative to gross mineralization and nitrification has not been widely examined in a variety of forest types or among ecosystems with varying soil N content. It has recently been suggested that immobilization of N is reduced in peatlands due to small microbial populations (Jonasson and Shaver 1999). However few, if any,

measurements of NH_4^+ and NO_3^- turnover have been made in northern peatlands. It is thus unclear whether the small NH_4^+ and NO_3^- pools in boreal conifer and peatland stands are rapidly cycled as the boreal forest is characterized by a relatively short growing season, cold temperatures, low atmospheric N deposition, low soil fertility and low net mineralization rates. Hence, simultaneous estimates of rates of gross mineralization and N immobilization are needed to better understand how these processes interact to regulate N retention in forested ecosystems.

Clearcutting may influence both the abiotic and biotic processes that control the consumption and release of N within forest soils. The importance of net nitrification relative to mineralization has been shown to greatly increase following clearcutting (Pedersen et al. 1999). Many researchers have found that net N mineralization rates are also stimulated following clearcutting, typically attributed to changes in soil temperature, moisture and C/N regimes (Vitousek et al. 1982; Munson and Timmer 1995; Paavolainen and Smolander 1998; Piatek and Allen 1999). This has ramifications for both the export of nitrate along hydrological flowpaths (Sollins and McCorison 1981; Krause 1982; Hill and Shackleton 1989; Devito et al. 1999) and soil fertility for successful forest renewal (Mou et al. 1993; Jurgensen et al. 1997). Research efforts focussed on net processes in temperate and boreal-temperate transitional upland forests have found elevated net N mineralization and nitrification, sometimes after a lag period (Vitousek et al. 1982; Munson and Timmer 1995; Paavolainen and Smolander 1998). However, it is unclear whether higher net rates following clearcutting are attributed to increased gross N mineralization rates and (or) decreased immobilization. Few studies have addressed the effects of clearcutting on microbial immobilization of N despite recent work demonstrating that microbial immobilization is a key factor regulating N loss from undisturbed forests (Davidson et al. 1992; Stottlemyer and Toczydlowski 1999; Berntson and Aber 2000). Although peatlands are potentially critical interfaces regulating N export from catchments due to their relative abundance and position in the landscape, the effects of clearcutting upland areas connected to peatlands on processes regulating peatland N retention have yet to be examined.

This research is part of a larger project examining N dynamics in boreal forest soils and at the potential changes in N dynamics as a result of clearcutting. The purpose of this

chapter is to investigate gross rates of N mineralization relative to net rates in the two main forest types in the Boreal Shield landscape -- conifer stands and peatlands -- and to determine if clearcutting alters gross N transformation rates. To address the hypotheses outlined below, I measured net and gross N mineralization and nitrification in uncut and recently logged conifer stands and peatlands in northwestern Ontario during August 1998. My results from net N incubation experiments conducted from 1996 to 1998 in undisturbed boreal forest soils show that this system has low soil N and that net mineralization and nitrification rates are low compared to other forest soils (see chapter 2). It is expected that these low rates are due to a combination of relatively high immobilization rates (i.e. fast turnover) or low gross mineralization rates. Secondly, I found higher net N mineralization in some peatlands than in some conifer stands (chapter 2). I hypothesized that the variability in net rates between forest types be due to differences in both gross N mineralization and immobilization rates. Lastly, others have postulated that higher net rates observed after clearcutting are due to reduced immobilization by the microbial community and not necessarily to changes in gross mineralization rates (e.g. Vitousek and Andariese 1986; Stark and Hart 1997). Thus I will test the following hypotheses: (1) clearcutting reduces rates of NH_4^+ and NO_3^- immobilization in conifer stands and peatlands; and (2) clearcutting does not alter gross N mineralization and nitrification rates in conifer stands and peatlands.

3.1 Study Site

This research was conducted in August 1998 at the Coldwater Lakes Experimental Watersheds (49°05'N and 92°10'W), situated on the Precambrian Shield in northwestern Ontario. The study site is located in the Boreal Shield region. Mean annual precipitation in nearby Atikokan is 550 mm with 173 mm falling as snow (Beaty 1998). April to October rainfall was 506 mm in 1998 and water equivalency of the late winter snowpack was 5 mm in 1998 (C. Allan unpubl. data). The mean January and July air temperatures are –17.6°C and 19.2°C, respectively (R. Steedman, unpubl. data). Average N deposition (1970-1982) at the Experimental Lakes Area (ELA), about 350 km west of

the study site, is 2.0 ± 0.8 kg/ha of NH_4^+-N and 1.8 ± 0.5 kg/ha of NO_3^--N (Linsey et al. 1987).

The bedrock geology of the study area is Archean granitic-gneissic and the Hartmann moraine runs along the southwest section of the study region (Zoltai, 1965). Conifer soils in the study area are classified as orthic dysteric brunisols. In general, the bouldery glacial till is patchy and thin near the top of hillslopes and up to 1 m at the bottom of hillslopes. The acidic forest floor (LFH horizon) is generally between 3 and 8 cm thick in uncut stand and is 0 to 8 cm thick in logged stand. Mineral layers are comprised of silty loam to coarse sand and are probably of glacial-fluvial origin. The top 20 cm of the peatland soils consist of a fibrous root mass, underlain by partially-decomposed, fibric organic material, and covered by thick moss (*Sphagnum* sp.) mats. Peat depth (to bedrock) is generally 40 cm at each site in the logged peatland and varies between 50 and 103 cm in the uncut peatland.

The study stands are unburned for the last 80-120 yrs. The major tree species in the uncut conifer stands are jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP), with a sparse understory of green alder (*Alnus viridis*). Before clearcutting, the logged conifer stand had a similar canopy structure to the uncut conifer stand. Black spruce with some black ash (*Fraxinus nigra* Marsh.) and an understory of the shrubs *Ledum groenlandicum* and *Gaultheria hispidula* dominate the uncut peatland and the logged peatland before harvesting. Trees were removed from the logged conifer stand and peatland mainly with chainsaws (Buchanan Forest Products Ltd.) in mid June 1998. Logs were dragged to loading docks with cable skidders. Regenerating vegetation on the logged peatland includes various graminoids, sedges and sparse *Sphagnum* clumps on hummocks. Various soil properties and water table elevations for the uncut and logged peatlands and conifer stands are presented in Table 3-1.

Table 3-1: Means (± SE) of selected soil properties in uncut and cut conifer stands and peatlands.

	Bulk Density Mg/m^3	Acidity[1] pH	Volumetric Water m^3/m^3	Water Table[2] cm	Soil Temperature °C
Peatland					
uncut	0.06 (0.004)	3.84 (0.08)	0.46 (0.02)	-25.5	15.1 [a] (0.5)
logged	0.15 (0.03)	3.83 (0.05)	0.51 (0.03)	-0.3	17.7 [b] (0.3)
Conifer Forest Floor					
uncut	0.10 [a] (0.01)	3.70 [a] (0.06)	0.07 [a] (0.01)	dry to bedrock	16.9 [a] (0.4)
logged	0.18 [b] (0.02)	3.99 [b] (0.06)	0.19 [b] (0.03)	dry to bedrock	18.9 [b] (0.5)
Conifer 0-10 cm Mineral					
uncut	0.40 [a] (0.04)	3.66 [a] (0.06)	0.11 (0.03)	dry to bedrock	13.4 [a] (0.5)
logged	0.52 [b] (0.04)	3.97 [b] (0.13)	0.17 (0.02)	dry to bedrock	17.1 [b] (0.2)

[1]determined by a 5:1 water:soil slurry
[2]Height of water table relative to ground surface the week before soil incubation; no standard error on estimates
ND indicates no data
Different letters represent significant difference between uncut and cut soils within a forest type, determined using a two-sample t-test, adjusting the probabilities for multiple comparisons with the Bonferroni test.

3.2 Methods

3.2.1 Experimental design

A catchment containing conifer uplands and peatlands was logged in June 1998. Nearby uncut conifer upland and peatland (within 1.5 km) with similar vegetation and soil properties were selected. One transect with seven sites, spaced 10 m apart, was set up in each uncut and logged conifer stand and peatland (Figure 3-1). Soil cores were sampled with a 4 cm diameter stainless steel corer at the forest floor (LFH horizon) and 0-10 cm mineral (A_e, where present, and B_f horizons) in the conifer stands and at 0-10 cm in the peatland hollows. At each site that soil cores were collected, temperature was measured at the beginning of the soil incubation period with a thermistor probe midway at each soil depth. Groundwater levels were measured at the beginning of the soil incubation period in one or two wells placed along the transects in both peatlands and the logged conifer stand. One soil pit (40 cm to bedrock) was dug to the bedrock in the uncut conifer stand the same week soil incubations were conducted. The pit did not intersect the water table.

3.2.2 Measurement of net rates

Inorganic N content was estimated for each soil core at seven sites along 1 transect in each cut and uncut conifer stand and peatland at the start and finish of a 24 d incubation. Soil cores were incubated in 0.025 mm polyethylene bags in their place of origin. Soil cores were kept on ice in the field and returned to the field laboratory where they were kept refrigerated until processing, within 12 h of sampling. Inorganic N in an approximately 5 g (dry mass) sub-sample of either the initial or incubated soil core was extracted with 50 mL 2 M KCl and shaken mechanically for 1 h to obtain equilibrium. Methods of subsequent laboratory analysis of both unlabeled and labeled KCl extracts are described in detail below (section 3.2.4).

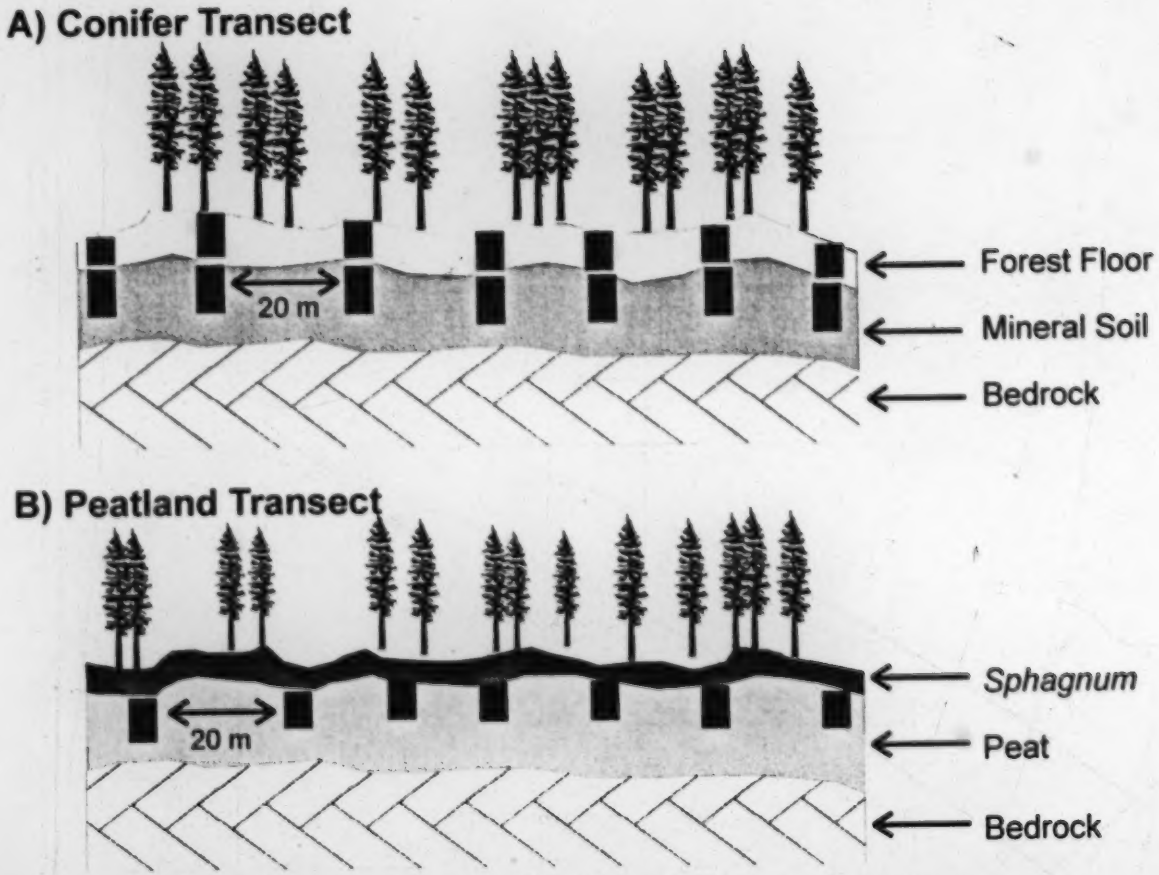

Figure 3-1: Schematic cross-section of a transect in the A) conifer and B) peatland forest types. Black rectangles represent location of soil cores. Soil cores are generally 10 cm long, except when the forest floor is < 10 cm thick.

3.2.3 Field labeling of intact cores

Gross mineralization and nitrification rates were estimated at the same sites as net rates in mid-August 1998. Four soil cores, obtained by inserting a polyethylene bag in a hand held bulb corer and twisting down to the desired depth, were labeled at each site. Two were amended with 30 mg N L^{-1} $(^{15}NH_4)_2SO_4$ and two with a solution containing 30 mg N L^{-1} $K^{15}NO_3$. The solutions, which contained 98 atom % ^{15}N enrichment, were injected from the bottom end of the core. Each core received six 1 mL injections, made with a 1 mL syringe. A corrected volume was used for sites where the forest floor in the conifer stands was thinner than 10 cm. During depression of the plunger, the syringe was slowly lifted up while being twisted to aid in even dispersion of label throughout the soil core. To ensure that the soil core stayed intact during injection of the labeled N solution, injection occurred while the bag was still in the corer.

One core of each labeled pair was immediately homogenized in the plastic bag and a 10 g (peatland soils) or 15 g (conifer soils) sub-sample was extracted with 50 mL (peatland soils) or 75 mL (conifer soils) 2M KCl. The other core from each pair was reburied and incubated *in situ* for 48 h before extraction. A 48 h incubation period was used to compensate for expected low gross mineralization rates.

Use of the polyethylene bag, instead of a standard PVC cylinder (Hart et al. 1994b), was employed because Canadian Shield soils are thin and plagued by numerous boulders, making coring difficult. This method also allowed for a more accurate determination of the organic-mineral soil interface in the conifer stands and created the least soil disturbance while maintaining the structure of the soil core.

3.2.4 Laboratory analyses

The KCl extracts of N from soil cores in the net and gross mineralization studies were filtered through pre-rinsed 45 μm Fisherbrand filter paper and frozen. An aliquot of the unlabeled and labeled extracts was analyzed for NH_4^+-N and NO_3^--N content on a Technicon autoanalyzer (Technicon 1973a,b). Estimates of net nitrification were determined by the difference in NO_3^--N content between the incubated and initial

unlabeled cores (Eno 1960). Net mineralization was estimated by the inorganic-N content (NH_4^+-N + NO_3^--N) of the incubated core minus that in the initial core.

The diffusion procedure described in detail by Hart et al. (1994b) was used to prepare KCl extracts for ^{15}N analysis. Some extracts were spiked with an appropriate amount of 50 μg/10 μL ^{14}N solution and (or) were diluted with 2M KCl prior to diffusion, to bring the % atom abundance down to 0.5-1.0 % and the N mass between 50 and 120 μg for more precise analysis. Mass spectrometer analysis of the glass filter disks was conducted at the Soil Biochemistry Lab, University of Alberta, Department of Renewable Resources.

Moisture was determined by oven drying (105°C for 24 h) a sub-sample of soil from each sampling site and depth, with percent moisture equal to the gravimetric water multiplied by the soil bulk density. Bulk density was calculated from the dry mass/total core volume. Soil acidity was measured as pH in a 5:1 water:soil slurry with a glass electrode. Soil pH for the uncut peatland was estimated from other uncut peatlands in the study area, discussed in chapter 2.

3.2.5 Gross Calculations

To calculate the fraction of ^{15}N recovered from a soil core at time zero or at time 48 h, the following equation from Hart et al. (1994b) was used:

$$F_{15N} = \frac{^{15}N \text{ excess (mg/kg)} * \text{core mass (kg)}}{^{15}N \text{ injected (mg)}}$$

where

^{15}N excess = (atom % ^{15}N enrichment of the N pool minus the background enrichment of ^{15}N) multiplied by the N pool size, divided by 100%.

^{15}N atom % enrichment = mole fraction of ^{15}N to $^{14+15}N$ * 100%.

Daily rates of gross mineralization and consumption were calculated using the following equation developed by Kirkham and Bartholomew (1954):

For $m \neq c$:

$$m = \frac{[NH_4^+]_0 - [NH_4^+]_t}{t} \times \frac{\log(APE_0/APE_t)}{\log([NH_4^+]_0/[NH_4^+]_t)}$$

$$c_A = m - \frac{[NH_4^+]_t - [NH_4^+]_0}{t}$$

Note: where m was negative, calculation of c_A used m = 0.

For m = c:

$$m = c_A = ([NH_4^+]_0/t)\ \ln(APE_0/APE_t)$$

where m = gross N mineralization (mg N kg^{-1} soil d^{-1})
c_A = NH_4^+ consumption rate (mg N kg^{-1} soil d^{-1})
t = time (2 d was used here)
APE_0 = atom % excess of NH_4^+ pool at time 0
APE_t = atom % excess of NH_4^+ pool at time t
$[NH_4^+]_0$ = total NH_4^+ concentration (mg kg^{-1}) at time 0
$[NH_4^+]t$ = total NH_4^+ concentration (mg kg^{-1}) at time t

Gross nitrification and NO_3^- consumption were calculated using the above equations, substituting n for m and c_N for c_A. The NH_4^+ immobilization rate was calculated by subtracting gross nitrification from gross NH_4^+ consumption. Gross NO_3^- immobilization was equivalent to gross NO_3^- consumption, as denitrification was assumed to be negligible over the short incubation period.

Calculating gross rates of NH_4^+ and NO_3^- immobilization using the ^{15}N dilution technique may overestimate immobilization as the substrate of these processes must be added to estimate these rates (Hart et al. 1994a, b). Consequently, gross N immobilization was also estimated from the difference between gross N mineralization and net N mineralization. Similarly, gross NO_3^- immobilization was estimated from the difference between gross nitrification and net nitrification. The two methods of calculating gross NH_4^+ and NO_3^- immobilization were then compared.

3.2.6 Statistics

Differences in NH_4^+ and NO_3^- net and gross mineralization rates, immobilization rates and soil N among peatland, conifer forest floor and conifer 0-10 cm mineral soils, between uncut and logged stands and their interaction were determined using analysis of variance. When ANOVA indicated a significant forest type effect, differences between means were tested using Bonferroni contrasts. Significant differences in net and gross

mineralization rates, immobilization, pool turnover time and selected soil properties between uncut and logged stands within each forest type were assessed using two-sample t-tests, adjusting the probabilities for multiple tests using the Bonferroni test. Regression analyses were used to test differences between the two methods of calculating N immobilization, gross N production vs. gross N immobilization rates, and net vs. gross mineralization rates. All tests were performed using SYSTAT version 9 (SYSTAT Inc. 1998).

3.3 Results

3.3.1 Recovery of ^{15}N label

Recovery of $^{15}NH_4^+$-N at time zero (10-15 min. after injection) was lower than recovery of $^{15}NO_3^-$-N in the conifer stand soils, but similar in the peatland soils (Table 3-2). No significant differences in $^{15}NH_4^+$-N or $^{15}NO_3^-$-N recovery were measured among forest types, or between uncut and logged soils within a forest type. There was high variability in the recovery of $^{15}NH_4^+$-N in the time zero soil cores and moderately high variability in the recovery of $^{15}NO_3^-$-N in the time zero cores within each forest type. Lower variability was observed in the soil cores incubated for 48 h compared to the time zero cores. After the soils were incubated for 48 h, mean recovery of $^{15}NH_4^+$-N and $^{15}NO_3^-$-N was 20-90 % lower than in the time zero cores.

3.3.2 Soil N and N transformation rates

Soil NH_4^+ in the logged conifer stand, at both soil depths, was more than twice that in the uncut stand (Table 3-3). In contrast, similar soil NH_4^+ was observed between the logged and uncut peatlands (Table 3-3). Ammonium availability was 1.7 to 30 times larger in the peatlands than in the conifer stands. Nitrate availability was very low and similar between the two forest types (Table 3-3). No difference in NO_3^- between uncut and logged stands was observed. Ammonium was 50 to 100 times larger than NO_3^-.

Table 3-2: Percentage of injected $^{15}NH_4^+$ and $^{15}NO_3^-$ retrieved from initial and incubated soil cores. Values are means with standard errors in parenthesis.

	Initial Recovery (initial core)		Final Recovery (incubated core)	
	$^{15}NH_4^+$	$^{15}NO_3^-$	$^{15}NH_4^+$	$^{15}NO_3^-$
Peatland				
uncut	58.7 (15.0)	63.0 (8.0)	17.8 (5.5)	41.2 (9.2)
logged	105.4 (13.5)	81.9 (5.5)	14.2 (4.6)	9.3 (5.1)
Conifer Forest Floor				
uncut	54.2 (10.5)	83.9 (7.7)	7.8 (2.9)	34.3 (7.1)
logged	63.7 (10.4)	93.2 (7.4)	51.0 (4.8)	60.7 (9.4)
Conifer 0-10 cm Mineral				
uncut	55.7 (11.0)	106.2 (18.4)	11.2 (3.9)	39.1 (7.9)
logged	64.6 (15.2)	106.7 (13.0)	34.4 (13.5)	47.1 (8.0)

Table 3-3: Mean (SE) inorganic N, net rates, gross rates and N turnover for uncut and cut forest soils. Different letters denote a significant difference between uncut and cut soils within a forest type at α=0.05. n=7.

	Soil N (mg/kg soil)		Mineralization (mg/kg soil/d)		Nitrification (mg/kg soil/d)		N Turnover (d)	
	NH_4^+	NO_3^-	Net	Gross	Net	Gross	NH_4^+	NO_3^-
Peatland								
uncut	29.66 (6.38)	0.26 (0.09)	-0.05 (0.50)	18.94 (4.65)	0.06 [a] (0.03)	1.65 (1.95)	1.65 (0.40)	0.04 (0.02)
logged	28.05 (8.70)	0.13 (0.05)	1.05 (0.82)	19.5 (7.39)	0.006 [b] (0.003)	1.27 (0.18)	1.42 (0.22)	0.01 (0.01)
Conifer Forest Floor								
uncut	8.44 (2.00)	0.08 (0.02)	0.26 (0.11)	14.84 (5.53)	-0.004 (0.003)	-0.11 [a] (0.15)	0.79 (0.24)	0.15 (0.09)
logged	19.94 (8.25)	0.11 (0.07)	-0.97 (1.33)	19.32 (13.48)	0.001 (0.01)	0.32 [b] (0.10)	6.00 (4.16)	0.04 (0.02)
Conifer 0-10 cm Mineral								
uncut	0.85 [a] (0.21)	0.02 (0.01)	0.05 [a] (0.02)	2.68 (0.61)	-0.004 [a] (0.002)	0.02 [a] (0.08)	0.57 (0.20)	0.02 (0.02)
logged	3.68 [b] (0.91)	0.01 (0.01)	-0.13 [b] (0.07)	1.56 (1.68)	0.001 [b] (0.002)	0.29 [b] (0.05)	1.29 (0.40)	0.00 (0.00)

Net mineralization rates were similar in the peatland and conifer forest stands (Tables 3-3 and 3-4). No difference was observed between the uncut and logged peatlands and forest floor soil in the conifer stands due to high within-transect variation. Rates of net mineralization in the uncut 0-10 cm conifer soils were significantly higher than in the logged soils. Net nitrification rates were significantly lower in the logged peatland compared to the uncut peatland (Tables 3-3 and 3-4). Rates of net nitrification in the logged conifer stand tended to be higher than in the uncut conifer stand, but were significantly different only in the 0-10 cm soils.

Gross mineralization and nitrification rates were generally 10 to 100 times larger than net rates. Gross mineralization rates in the conifer 0-10 cm mineral soils were six times lower than in the forest floor soils and peatlands (Tables 3-3 and 3-4). There were no statistically significant differences in gross mineralization rates between uncut and logged forest soils.

Although gross nitrification rates were a factor of ten higher in the peatlands compared to the conifer forest floor and 0-10 cm mineral soils (Tables 3-3), the non-significant relationship (Table 3-4) likely resulted from high variation observed in the uncut peatland. There was no observed difference in gross nitrification rates between the uncut and logged peatlands, although this was due to 1 high value in the uncut peatland. All other gross nitrification rates in the uncut peatland were not significantly different from zero ($P > 0.10$). Gross nitrification rates were significantly greater in the logged conifer stand, at both depth increments, than in the uncut conifer stand.

Turnover of NH_4^+ was generally less than 2 d in each of the peatland and conifer forest floor and 0-10 cm mineral soils, with the exception of two sites in the LFH of the logged conifer stand (Tables 2-3). Rapid turnover of NO_3^- was measured in all soils and no differences among forest types were observed. Neither turnover of NH_4^+ nor NO_3^- showed any significant difference between uncut and logged stands, although turnover of NO_3^- tended to be slightly faster in each logged stand (Table 2-4).

Immobilization rates as calculated by the isotope dilution measurements (isotope method) and those calculated independently through the difference between net and gross rates (difference method) were closely related for NH_4^+ immobilization ($r^2 = 0.53$, $P < 0.001$) and NO_3^- immobilization ($r^2 = 0.641$, $P < 0.001$) (Table 3-5). The slope of the

Table 3-4: Results of analysis of variance (p-values presented) of various N cycling rates for uncut and clearcut conifer stands and peatlands.

	P-values		
Soil Variable	**Forest Type**	**Clearcutting**	**Interaction**
NH_4^+	<0.001	0.361	0.501
NO_3^-	0.006	0.396	0.282
Net mineralization	0.449	0.851	0.241
Net nitrification	0.009	0.143	0.025
Gross mineralization	0.040	0.818	0.916
Gross NH_4^+ immobilization*	0.038	0.818	0.842
Gross nitrification	0.346	0.904	0.919
Gross NO_3^- immobilization*	0.369	0.892	0.933
Turnover NH_4^+	0.313	0.174	0.229
Turnover NO_3^-	0.114	0.109	0.476

* immobilization rates were calculated from the respective gross rate minus the net rate

Table 3-5: Mean (SE) immobilization calulated using the isotope dilution method and the difference between gross and net rates. Different letters denote significant difference between uncut and cut soils within a forest type at α=0.05. n=7.

	Immobilization mg/kg/d (isotope dilution)		Immobilization mg/kg/d (difference method)		% N Immobilization*	
	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-
Peatland						
uncut	9.85 (2.50)	3.65 (2.14)	19.10 (4.86)	1.58 (2.0)	56.6 (14.2)	89.2 (10.7)
logged	18.16 (8.90)	3.79 (1.17)	18.07 (7.00)	1.26 (0.18)	86.5 (18.6)	99.5 (0.4)
Conifer Forest Floor						
uncut	10.82 (1.82)	1.82 (0.58)	14.58 (5.54)	-0.10 [a] (0.15)	102.4 (21.1)	83.3 (14.7)
logged	14.68 (8.56)	0.88 (0.50)	20.40 (13.13)	0.31 [b] (0.11)	270.0 (145.6)	85.7 (14.9)
Conifer 0-10 cm Mineral						
uncut	3.35 (0.97)	0.49 (0.13)	2.63 (0.59)	0.03 [a] (0.08)	130.5 (19.7)	100.0 (1.6)
logged	2.43 (1.06)	0.53 (0.11)	1.68 (1.67)	0.29 [b] (0.05)	76.5 (20.9)	99.2 (0.8)

* calculated using N immobilization (difference method) divided by gross mineralization multiplied by 100%.

line representing the two methods of calculating NH_4^+ immobilization was significantly different from one (mean $\pm$ 1SE = 0.55 $\pm$ 0.09), while for NO_3^- immobilization the slope of the regression line was not significantly different from one (mean $\pm$ 1SE = 1.04 $\pm$ 0.14) (regressions not shown). Comparisons of N immobilization rates among forest types and uncut and logged stands will hereafter be made using only the difference method because there is some evidence for overestimation of immobilization rates using the isotope dilution method.

Rates of NH_4^+ immobilization exceeded rates of NO_3^- immobilization (Table 3-5). Ammonium immobilization rates were lowest in the conifer 0-10 cm mineral soils, intermediate in the conifer forest floor soils, and highest in the peatlands. Rates of NH_4^+ immobilization did not significantly differ between the uncut and logged soils in any of the forest types.

Although gross NO_3^- immobilization rates were a factor of ten higher in the peatlands compared to the conifer forest floor and 0-10 cm mineral soils (Tables 3-5), the non-significant ANOVA (Table 3-4) likely resulted from high variation observed in the uncut peatland. Nitrate immobilization rates were similar between uncut and logged peatland and LFH conifer forest soils, but NO_3^- immobilization rates were significantly higher in the logged 0-10 cm mineral conifer soils than the uncut soils. In all forest soils, percent NH_4^+ and NO_3^- immobilized relative to N produced through mineralization and nitrification was not significantly different from 100% (Table 3-5).

Soil moisture was very weakly, positively correlated with gross mineralization rates (r^2 = 0.142, P = 0.021) and NH_4^+ immobilization rates (r^2 = 0.141, P = 0.022), but not to gross nitrification or NO_3^- immobilization rates. Net and gross mineralization rates were not significantly correlated (P = 0.15), nor were net and gross nitrification rates (P = 0.55). Ammonium immobilization rates were positively correlated to NH_4^+ (P = 0.048) and NO_3^- was related to NH_4^+ (P = 0.015).

3.4 Discussion

Based on soil N and net mineralization and nitrification rates, N cycling in the Boreal Shield forest is very low compared to other boreal forests and also to temperate,

alpine tundra, and tropical forests (Binkley and Hart 1989; Foster 1989; Hill and Shackleton 1989; Zak and Grigal 1991; Fisk and Schmidt 1995; Chapin 1996; Humphrey and Pluth 1996; Devito et al. 1999; Ohrui et al. 1999). As with other studies however (Davidson et al. 1992; Hart et al. 1994a; Stottlemyer and Toczydlowski 1999; Chen and Stark 2000), gross rates of mineralization and nitrification in both the conifer stands and peatlands were significantly greater than net rates. Hence, gross rates seem to poorly predict net rates, even in forests with low soil N content, such as soils at this study site.

Few estimates of gross mineralization and nitrification rates exist to which these data can be compared, particularly for the peatland soils. The gross mineralization, nitrification and NH_4^+ turnover rates observed for these soils are comparable to the range of rates available for selected temperate forest, boreal forest and grassland soils (Davidson et al. 1992; Wessel and Tietema 1992; Stark and Hart 1997; Neill et al. 1999; Stottlemyer and Toczydlowski 1999; Chen and Stark 2000). However, NO_3^- turnover rates are much faster in these soils than that recorded for the previously mentioned forest soils, signifying the extreme NO_3^- limitation in these soils. It appears that contrasts in net mineralization and nitrification rates among different forest types and regions may be a function of differing percent immobilization rather than dissimilar gross production rates.

As expected, low net mineralization rates appear to be due to NH_4^+ immobilization rates equivalent to gross mineralization rates. Rates of gross mineralization and NH_4^+ immobilization in the peatlands are as high or higher than in the conifer stand soils. High peatland NH_4^+ immobilization in this study contrasts with the findings of Verhoeven et al. (1990), which suggest reduced or absent N immobilization in *Sphagnum*-derived organic matter. My results indicate that conifer stands and peatlands in this area have similar N turnover, despite differences in soil water content, N content and vegetation cover. Although the soils are derived from different substrates, they seem to have similar quality.

Clearcutting does not seem to stimulate gross mineralization rates in either the peatland or conifer forest soils. This is not expected based on comparisons of young vs. old conifer forests where rates of gross mineralization and N turnover are higher in older forests (Vitousek and Andariese 1986; Davidson et al. 1992). However, differences in gross mineralization rates between young and old forests in the previously mentioned

studies were associated with differences in soil quality and fertility. The uncut and logged forest soils in my study had similar N content and soil properties, thus few differences may be expected.

Gross nitrification rates were below detection in the uncut conifer stand, while low rates were measured in the uncut peatland, logged peatland and logged conifer stand. Negative production or immobilization rates are impossible and are due to variability between soil cores. Negligible net nitrification rates in each forest type can be attributed to a 100 % immobilization of the NO_3^- produced. The role of a fast vs. slow immobilization pathway (Berntson and Aber 2000) regulating high NO_3^- retention of the small amount of NO_3^- produced in these soils is unclear. Relatively low gross nitrification and high NO_3^- immobilization suggests that nitrifier populations in the conifer stands may be small, or that nitrifiers are relatively poor competitors for NH_4^+.

Many researchers have concluded that NO_3^- production and immobilization are prevented in peatland soils with generally anoxic conditions, low pH, N-poor soil conditions and low soil temperature (Nieminen 1998; Chapin 1996). Measurements of negative net nitrification rates at this study site and other study sites suggests that low gross nitrification and high immobilization rates limit soil NO_3^- pools (Chapter 2; Hill and Shackleton 1989; Devito et al. 1999). Gross nitrification rates measured in uncut and logged peatlands in my study do not support low or no nitrification occurring in peatlands. These data are some of the first evidence for gross nitrification and immobilization rates occurring in water-logged peat soils that have low N content, are acidic and have relatively cold soil conditions. The peatland gross nitrification rates measured here are similar to rates measured for the conifer forest floor soils and also for aerobic soils in other conifer and some deciduous forested ecosystems (Wessel and Tietema 1992). Similar gross nitrification rates among peatland and upland areas despite differences in soil water content, temperature and organic matter content suggests NH_4^+ availability, rather than environmental factors, probably limit gross nitrification rates at this study site.

Higher gross rates of NH_4^+ immobilization than NO_3^- immobilization found here have also been found in other studies (Vitousek and Andariese 1986; Davidson et al. 1992). However, the importance of NO_3^- in N cycling in the Boreal Shield forest should

not be minimized. The NO_3^- immobilization rates calculated from the isotope dilution technique were almost always as high as gross nitrification rates, regardless of the forest type. Although the high immobilization rates may be due to substrate addition (Davidson et al. 1991), similar results were calculated from independent estimates of gross and net nitrification rates. Regardless, these results clearly indicate a higher capacity for NO_3^- immobilization than the NO_3^- produced. Also, the turnover of NO_3^--N was less than 0.15 d in peatland and conifer soils, indicating rapid movement of NO_3^- through a small pool. These results suggest that the potential for leaching of NO_3^- under natural and disturbed conditions is very low.

The gross nitrification and immobilization rates were significantly higher in the logged compared to the uncut conifer stand at both soil depths. The higher temperature in the logged stand may partly explain the increased immobilization rates. However, the higher soil moisture of the logged stand would be expected to decrease the aerobic process of gross nitrification. The interactive effects of higher soil temperature and moisture in the logged stand compared to the uncut stand is unclear. Another factor potentially regulating gross nitrification rates is the presence of allelochemical inhibitors released by plants to the uncut conifer soils compared to the logged conifer soils. Frazer et al. (1990), suggest that lower nitrifier activity in a forested control site compared to 5 and 17 yr old regeneration sites may be attributed to several free-organic acids present, presumably phenolics, in the forest litter at the control site. The inhibition of nitrification by soil polyphenols has been previously demonstrated (Olson and Reiners 1983). Further tests are needed to understand the role of polyphenols in inhibiting gross nitrification.

Incomplete recovery of the added $^{15}NH_4^+$ label in the time zero conifer soil cores may be accounted for by abiological uptake mechanisms. The fixation of $^{15}NH_4^+$ to clay and possible binding to soil organic matter are probable consumptive processes (Davidson et al. 1991; Strickland et al. 1992; Liang et al. 1999; Murphy et al. 1999). In contrast, abiotic uptake of $^{15}NO_3^-$ was negligible in the uncut and logged conifer forest floor and 0-10 cm mineral soils. Incomplete recovery of the added NO_3^- in the peatlands may be due to abiotic immobilization or poor soil homogenizing before extraction of N with KCl. However, soils were well homogenized before extraction. Potential abiotic NO_3^- immobilization mechanisms include nitrosation reactions (Azhar et al. 1986) or

unknown mechanisms. However, it is questionable whether uptake of $^{15}NH_4^+$ and $^{15}NO_3^-$ within the peatlands is solely abiotic as significantly higher recoveries of the added ^{15}N labels were measured in the logged peatland compared to the uncut peatland. Williams et al. (1999) found high uptake of N by two *Sphagnum* species treated with $^{15}NH_4{}^{15}NO_3$. Higher uptake of ^{15}N in the uncut peatland soils in my study may be due to inclusion of living, non-photosynthetic moss tissue in the soil cores. It is recommended that further studies should be undertaken to clarify abiotic uptake of N in both the conifer and particularly the peatland soils of this site.

3.5 Conclusions

Similar rates of gross mineralization and NH_4^+ immobilization were observed in uncut and logged peatland and conifer soils. These results confirm interpretations made from the net mineralization findings presented in chapter 2. Gross nitrification rates may be higher in logged than uncut peatland soils, however, findings were inconclusive due to high variability in rates among sites within the uncut peatland. Gross nitrification was absent in the uncut conifer stand soil and significantly higher in the cut conifer stand soils. Although clearcutting appeared to increase gross nitrification rates in conifer soils, these results were not transferred to net rates, as NO_3^- immobilization is essentially 100 % due to NO_3^- limited conditions. Turnover of NH_4^+ and NO_3^- was very rapid, usually less than one day, in the peatlands and conifer stands. The factors limiting mineralization and nitrification rates seem to be important in this ecosystem; thus future research should be directed toward understanding these limits. These data imply a low potential for nitrate losses post-harvest and no change in the N available for regenerating vegetation.

3.6 References

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CHAPTER 4: GENERAL CONCLUSIONS

4.0 Implication of Findings for Forest N Export

Microbial immobilization has recently been shown to be an important mechanism regulating N retention in undisturbed temperate and temperate-boreal transitional forests (Stark and Hart 1997; Stottlemyer and Tocyzlowski 1999; Berntson and Aber 2000). The very high NH_4^+ and NO_3^- immobilization rates presented here, combined with low net mineralization and nitrification rates are evidence for a similar mechanism retaining N in Boreal Shield forests.

Many studies have shown that logging increases NO_3^- leaching from soils and thus N export to adjacent water bodies (Likens et al. 1978; Vitousek et al. 1979; Sollins and McCorison 1981; Krause 1982; Feller and Kimmins 1984; Hendrickson et al. 1989). These increases are attributed to an increase in the importance of rates of nitrification relative to mineralization rates (e.g. Vitousek et al. 1982; Vitousek and Andariese 1986; Munson and Timmer 1995). Measurements of low net and gross N transformations suggests that the conifer, deciduous and peatland soils at the Coldwater Lakes Experimental Watersheds suggest soils are N-poor and that rates are minimally, if at all, affected by clearcutting. Thus although most studies have shown that disturbance through clearcutting causes increased N loss to streams and lakes, the potential for N loss post-harvest is limited at this study site.

4.1 Implications of Findings for Forest Regeneration

It has been widely held that increased nitrification of soil NH_4^+ in clearcuts, leading to higher soil NO_3^-, may contribute to poor conifer regeneration in plantations (Montaginini et al. 1986) as conifers discriminate against NO_3^- and prefer NH_4^+ (Lavoie et al. 1992; Kronzucker et al. 1997). It is unlikely that clearcutting caused a shortage of the preferred form of N for conifer forest regeneration at my study site as soil NH_4^+ either remained constant after clearcutting or was higher in clearcut stands compared to uncut stands and both net and gross mineralization rates were unaffected by clearcutting.

However, the low soil N fertility measured at this site compared to other forested ecosystems may have serious implications for forest growth and rapid regeneration after disturbances such as logging or fire. Nitrogen uptake requirements for optimal growth of conifers and deciduous hardwoods, 30-75 kg/ha/yr and 50-100 kg/ha/yr, respectively (Gosz 1981), appear to be much greater than soil N reserves and replenishment rates (Figure 4-1). After logging, soil TN, mineralization rates and input of N from stumps and roots are insufficient to sustain rapid regeneration. With the plant uptake rates suggested by Gosz (1981) for healthy jack pine, soil N reserves would be depleted within 3-4 years. Recycling of N through litterfall may play an key role in tree nutrition in this ecosystem, and its importance warrants further investigation. Slow tree growth, especially during the early growth period, may also combat low soil N supply rates. Internal re-distribution of N within trees after the early growth period probably reduces the plant demand for N on soil nutrient reserves (Gosz 1981; Foster and Morrison 1987; Jonasson and Shaver 1999) and allows for economically viable wood production at this site.

Full-tree (above-ground phytomass) harvesting was conducted in the catchments at the Coldwater Lakes study site. Delimbing was executed at loading docks where slash was piled up and then burned in the fall of 1998. Implementing conventional harvesting (stems only), i.e. leaving slash on-site, instead of full-tree harvesting will reduce N removal during harvesting from an estimated 234 kg/ha to 62 kg/ha (Foster and Morrison 1987). Provided that N losses via leaching or gaseous removal are low when slash is left on-site, conventional harvesting may allow for more rapid regeneration of conifer species and potentially a shorter rotation time.

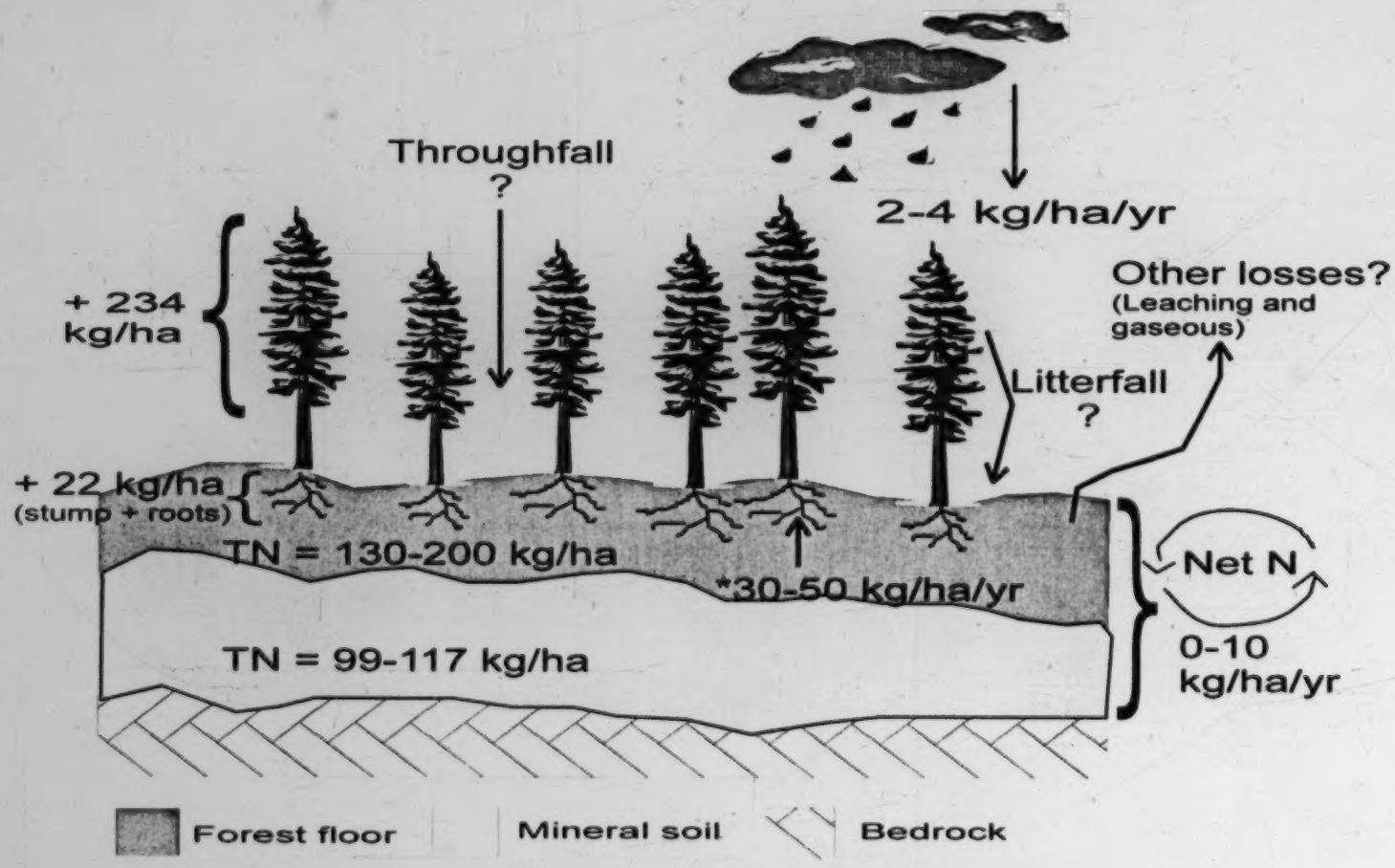

Figure 4-1: General nitrogen budget for a 100 yr old typical jack pine stand in the Coldwater Lakes Experimental Watersheds study region, showing the shortage of nitrogen required for optimal tree growth. * from Gosz (1981); + from Foster and Morrison (1987).

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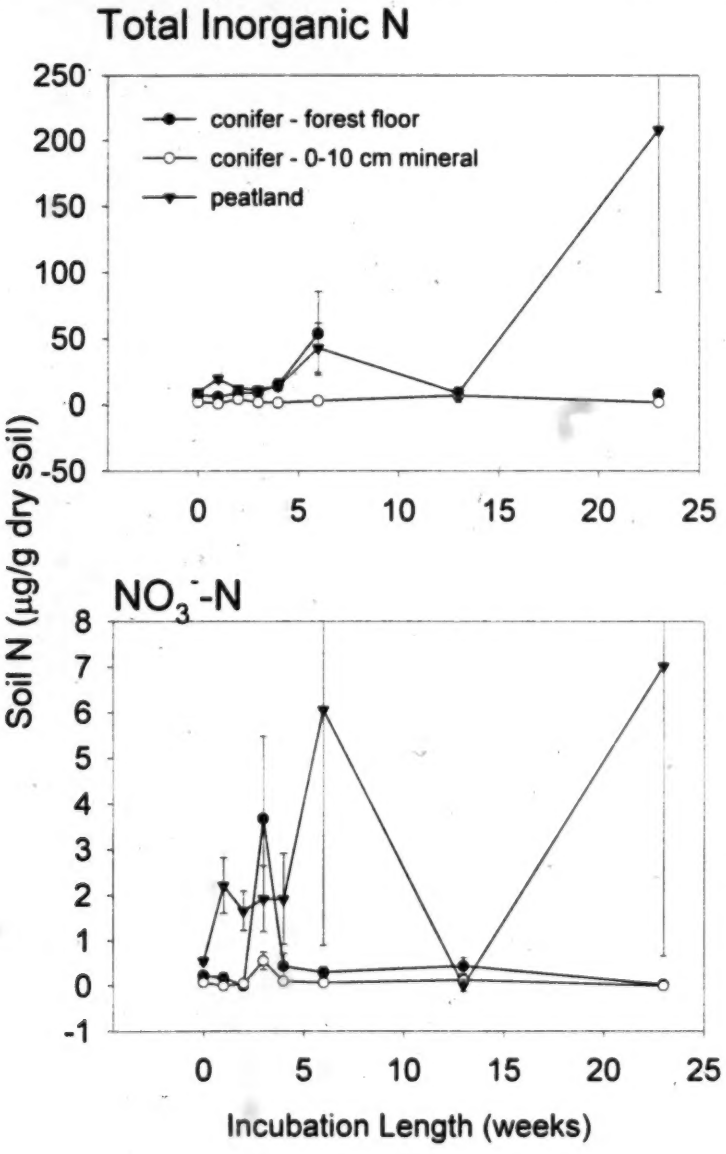
Appendix A: Change in soil total inorganic N and soil nitrate in buried bags incubated in a conifer stand and a peatland for various lengths of time for May through October 1998.



Appendix B: Mean (SE) extractable TIN, nitrate-N and bulk density for forest floor conifer soils 24, 48 and 72 h after samples were obtained. n=7. Letters indicate significant difference of $p<0.05$, as determined by one-way ANOVA, with a post-hoc Bonferroni test. Soils were left in a fridge before extraction.

Time Before Extraction	TIN	NO_3^--N	Bulk Density
h	ug/g dwt	ug/g dwt	g/cm^3
24	2.66 (0.67)[a]	0.05 (0.01)[a,b]	0.36 (0.06)[a]
48	1.89 (0.18)[a]	0.01 (0.002)[a]	0.60 (0.05)[a]
72	2.52 (0.73)[a]	0.05 (0.01)[b]	0.47 (0.08)[a]